RAPTOR RESEARCH

Volume 11

Number 1/2

Spring/Summer 1977

Raptor Research Foundation, Inc.
Provo, Utah, U.S.A.

RAPTOR RESEARCH Spring/Summer 1977

Volume 11, Number 1/2, Pages 1-48

CONTENTS

SCIENTIFIC PAPERS

RAPTOR RESEARCH

Published Quarterly by the Raptor Research Foundation, Inc.

The Raptor Research Foundation, Inc., welcomes original articles and short notes concerning both diurnal and nocturnal birds of prey. Send all papers and notes for publication and all books for review to the Editor. Most longer articles (20 or more typeset pages) will be considered for publication in *Raptor Research Reports,* a special series for lengthy and significant contributions containing new knowledge about birds or new interpretations of existing knowledge (e.g., review articles). However, authors who pay page costs (currently $20.00 per page) will expedite publication of their papers, including lengthy articles, by ensuring their inclusion in the earliest possible issue of *Raptor Research.* Such papers will be in addition to the usual, planned size of *Raptor Research* whenever feasible.

SUGGESTIONS TO CONTRIBUTORS: Submit all manuscripts in duplicate, typewritten, double spaced (all parts), on one side of 8½ x 11-inch paper, with at least 1 inch margins all around. Drawings should be done in India ink and lettered by lettering guide or the equivalent, if possible. Photographs should be on glossy paper. Avoid footnotes. Provide an abstract for all papers more than four double-spaced typed pages in length, not to exceed 5 percent of the total length of the paper. Keep tables at a minimum, and do not duplicate material in either the text or graphs. For advice concerning format refer to the Council of Biological Editors' Style Manual for Biological Journals or to previous issues of *Raptor Research.* Proofs will be sent to senior authors only. Major changes in proofs will be charged to the authors. Reprints should be ordered when proofs are returned.

COURTSHIP BEHAVIOR OF LARGE FALCONS IN CAPTIVITY

by
Peter H. Wrege
Tom J. Cade
Section of Ecology and Systematics
Langmuir Laboratory
Cornell University
Ithaca, New York 14853

Abstract

The courtship behavior of captive Peregrine Falcons (*Falco peregrinus*), Gyrfalcons (*Falco rusticolus*), Prairie Falcons (*Falco mexicanus*), and Lanner Falcons (*Falco biarmicus*) is very similar in basic form and function. No subspecific differences in courtship behavior were apparent in Peregrines. Variations in the vocalizations of a species are common and function to communicate the intensity of motivation. The seasonal ontogeny of Peregrine reproductive behavior is similar in all experienced pairs. Gradual and consistent shifts in yearly development are evident during the first two years of breeding, but usually a pattern appears to stabilize by the third year.

Major interspecific differences were found in the frequency of aggressive and nonaggressive postures in both ritualized and nonritualized Displays and in their relative use by the male and female. Evidence from the behavior of captives supports the idea that females are dominant in the pair relationship. The influence of size dimorphism on the development and maintenance of female dominance is reflected both interspecifically and intraspecifically in the relative frequencies of agonistic behavior. We suggest that potentially severe injury resulting from aggressive fighting, combined with a pair relationship dependent on female dominance, has resulted in a repertoire of postures highly efficient in communicating fine changes in motivation and a vocal repertoire that varies continually with the intensity of motivation.

Introduction

We have been studying the courtship behavior of paired falcons in captivity as one part of an attempt to understand how behavioral and physiological mechanisms function in the reproduction of raptorial birds, and how these mechanisms are influenced by environmental factors. Pairing and reproduction may involve special problems for highly predatory birds—especially in confinement—because they are usually solitary and pugnacious much of the year and because they possess formidable beaks and feet, as well as a strong motivation, for killing other animals. These include, in the case of large falcons, birds similar in size and shape to themselves. Potentially, a falcon represents a hazard to its mate. Given these conditions, important social processes must be brought into play to counteract these strong aggressive tendencies (Willoughby and Cade 1964).

Thus, social adjustments that take place for effective pair-bonding and integration between male and female falcons are particularly rewarding subjects for testing current theories about pairing and sexual selection (Brown 1975), as well as for providing new hypotheses for further study. Such studies can also contribute much to the basic knowledge needed to propagate Peregrine Falcons and other threatened or endangered species in captivity on a practical scale.

The purpose of this paper is to describe thoroughly the courtship Displays and associated behavior of mated falcons, to assign tentative functions to them, and to propose some hypotheses about the role of sexual size dimorphism in the pairing of large falcons.

Materials and Methods

We have examined four species of the genus *Falco* for this study: the Peregrine (*Falco peregrinus*), Gyrfalcon (*Falco rusticolus*), Prairie Falcon (*Falco mexicanus*), and Lanner Falcon (*Falco biarmicus*). The former three species breed in North America. Lanner Falcons breed mainly in arid parts of Africa where their ecology closely parallels that of Prairie Falcons. Our emphasis is on comparisons between the behavior of Peregrines and Gyrfalcons. Observations were made regularly for four seasons on captive pairs of Peregrines and for two seasons on captive Gyrfalcons.

Three pairs of Peregrines were studied in detail, two from northern Alaska (*F. p. tundrius*) and one from the Queen Charlotte Islands (*F. p. pealei*). These pairs have bred successfully for at least three years. Additional observations were made on three pairs from the western United States (*F. p. anatum*), two pairs from northern Quebec, and one pair each from Alaska (*F. p. tundrius*), Spain (*F. p. brookei*), and the Queen Charlottes (*F. p. pealei*). All these pairs attempted mating, and the females laid eggs. Behavioral observations were made in 1972 and 1973 from April through mid-June and in 1974 and 1975 from late January through May.

Three pairs of Gyrfalcons from northern Quebec were studied for two years. Only one pair produced young in 1974 and 1975. Observations were made from early January through April. The Gyrfalcons and arctic Peregrines (*F. p. tundrius*) were placed on a schedule of advancing photoperiods, as described by Weaver and Cade (1974). This schedule is timed for Peregrines so that all subspecies are roughly synchronized to begin egg-laying at about the same date. We made incidental observations over a three-year period on four to five productive pairs of Prairie Falcons and on two pairs of Lanner Falcons, one of which has produced multiple broods for four consecutive years.

There was no fixed schedule of observation during 1972 and 1973. In 1974 pairs were observed regularly five days per week and periodically on the other days. Study was concentrated between dawn and 1100 hours, and, twice per week, for three to four hours prior to darkness. These are periods of greatest activity. Pairs with advanced photoperiod were observed from the time the lights went on until 1100 hours. Additional observations were scattered throughout the day. Observations in 1975 were made from "dawn" until 1100 hours every day. Additional observations were made at other times of day, with emphasis on the hours before darkness.

Throughout our studies, the falcons were housed in the Cornell Behavioral Ecology Building, Ithaca, New York. Pairs were kept together throughout the year. This facility was equipped for about 35 pairs of falcons and their young. Chamber dimensions and fixtures were described by Weaver and Cade (1974). Visual exposure of the falcons to humans was minimal, and none of the falcons was tame enough to allow a human to enter its room without becoming alarmed. Feeding was accomplished through chutes at two levels. Dead four-week-old chickens and adult Coturnix Quail (*Coturnix coturnix*) were provided as food. Rooms had to be entered occasionally to change water baths and, when necessary, to examine the health of a bird. Observation through one-way mirrors was possible from two levels in each breeding chamber. In addition to handwritten notes, still photography and video-tape recordings were used for the analysis of behavior. In both cases, pictures were

taken through the one-way mirrors without additional illumination. Vocalizations were recorded with a Nagra IIIB recorder and an Altec microphone and were analyzed on a Kay Electric Sonograph with a wide-band filter.

Results

Behavior during the first successful breeding season for a pair has been deemphasized in our analysis of results. During the first year, reproductive behavior is often contracted into a short and accelerated courtship period. Behavior patterns appear identical to those of experienced pairs, but their frequencies and seasonal ontogeny are different. Captive Peregrines show no subspecific differences either in the patterns of behavior or in its ontogeny; however, sample sizes are too small to be certain there are no average differences that might be revealed by statistically treatable samples.

Nearly all behavior patterns described herein are displays in that they are signals that have become specialized for communication (Brown 1975). The sequencing of displays into larger recognizable units, with their own specialized signal, is very common in animals. In this paper these units have been given descriptive names which are capitalized and called Displays. The terms *display* and *posture* are used interchangeably for behavior patterns that make up or occur independently of the more complex Display units. The names of vocalizations are also capitalized.

Descriptions and Definitions of Behavior in Peregrine Falcons. Among the many behavior patterns of captive Peregrine Falcons, 13 Displays and a few other behaviors are particularly useful in describing the pair relationship and the seasonal ontogeny of reproductive behavior. Many of these have been at least partly described (e.g., for wild Peregrines–Cade 1960, Fischer 1968, Nelson 1970; for captive Peregrines–Fyfe 1972, Nelson and Campbell 1973, 1974, Weaver and Cade 1974). In this section we provide a descriptive sketch of these Displays in captive Peregrines with some detail (1) on those not previously described or (2) in cases when the behavior of our pairs was significantly different from published descriptions.

1. *Head-Low Bow Display.* Four variations of this Display occur in contexts ranging from anti-aggressive through mildly aggressive. They are exhibited by either sex in response to movement or close proximity of the mate. The basic mode of this Display is nonaggressive, and the postures it includes are characteristic of many sequences preliminary to and during close mutual interactions. These characteristics include holding the head below the body plane, beak directed away from the mate and usually toward the substrate, and generally sleeked plumage.

There are horizontal and vertical forms of this Display. The Horizontal Head-Low Bow involves crouching in a horizontal body position, the head bent at almost 90° to the body plane and the beak often contacting the substrate. The Vertical Head-Low Bow is a less intense form, given with the body in a normal perching position, but with the head depressed. Body positions intermediate between vertical and horizontal are frequently observed, and there is complete intergradation in the amount the head is bowed (fig. 1a). Either form of this Display may involve vigorous bowing up and down from the head-low position to a normal posture with the head above the body plane (see Nelson and Campbell 1973). Often the Head-Low Bow is maintained without vigorous bowing, especially when in close proximity to the mate. Several vocalizations may be given during the Display, including the Eechip and Whine vocalizations (figs. 2a and 2b). It is also frequently unaccompanied by calling. Mueller (1971) has described similar displays in the American Kestrel (*Falco Sparverius*).

A third variation of this Display is the Extreme Head-Low Bow (fig. 1b). Its function is anti-aggressive, and it appears to be a very intense form of the Horizontal Head-Low Bow described above. During this Display the body is tipped far forward so that the tail is very high and in line with the body. Slight bowing may be included, and the Eechip vocalization is frequently given. This Display apparently involves a mixture of two motivational states—fear and copulation. It is given most often by the female during Mutual Ledge Displays (see below) and especially just before aborted attempts to copulate. The general form of this Display is, in fact, quite similar to the female's Copulation Solicitation Display (see below).

The Agonistic Head-Low Bow is a fourth variation of the more general Head-Low Bow Display. This Display includes the "deep forward bow" described by Nelson and Campbell (1973). It is given by either sex in agonistic situations, and by the male in precopulatory behavior. Feathers on the head, especially on the sides, may be flared out, and feathers on the shoulders are often raised. The head is held below the body plane, but the beak is frequently directed at the mate. Horizontal and vertical body postures are used, the latter especially by the male during precopulatory display (see Hitched-Wing Display). Eechip or Chitter vocalizations sometimes accompany this Display (figs. 2a and 2c).

2. *Individual Ledge Displays.* Individual ledge displays are given by the male or female (Male Ledge Display or Female Ledge Display, respectively) alone on a prospective nest-ledge. They are usually centered on a scrape (a shallow depression made in the substrate). Basic behavior patterns were identical in all subspecies studied. Major differences involved vocal peculiarities, which may represent individual variation more than subspecific difference.

a. *Male Ledge Display*. The scrape is approached in a horizontal head-low posture accompanied by a continual Eechip vocalization (figs. 1a and 2a). When sexual motivation is high, a "high step" or "tippy-toe" gait is used and produces a side-to-side swagger (also described by Nelson and Campbell 1973 in another context). The horizontal head-low posture is maintained during intense activity at the scrape, and a complete Eechip vocalization is given repeatedly. Pauses begin after five to ten seconds, during which the male looks toward the female. At any time, movement by the female is likely to elicit renewed intense display, and her reaction determines the duration of display. At low intensity the male may become relaxed, and the vocalization then is usually an incomplete variation of the Eechip.

b. *Female Ledge Display*. Female Display differs from male Display in several ways. In general it is less intense and is sometimes difficult to distinguish from nondisplay activity on the nest-ledge. The postures are less distinctive and more variable. Approach is usually entirely horizontal (i.e., head, body, and tail all in one plane) or with a slight lowering of the head. A complete Eechip vocalization is given. The female turns around in the scrape, mandibulates debris on the ledge, and scrapes frequently (see below). Pauses to look at the male are infrequent. Female Ledge Displays often change into apparent noncommunicative activity.

3. *Mutual Ledge Display*. Simultaneous activity by both sexes on the nest-ledge, usually centered on a scrape, characterizes this Display. The most intense portion occurs just as both birds arrive at the scrape, each in the horizontal head-low posture with beaks close to the substrate, vigorously Eechipping. Movements of each sex relative to the other and the characteristic pauses that occur during the Display have been described by Nelson and Campbell (1973, 1974).

Interactions with movements, postures, and vocalizations identical to those in Mutual Ledge Displays may occur infrequently on perches other than the nest-ledge.

4. *Billing.* Billing is often seen during the longer Mutual Ledge Displays, and occasionally when the pair is perching very close together. Billing involves twisting the head sideways,

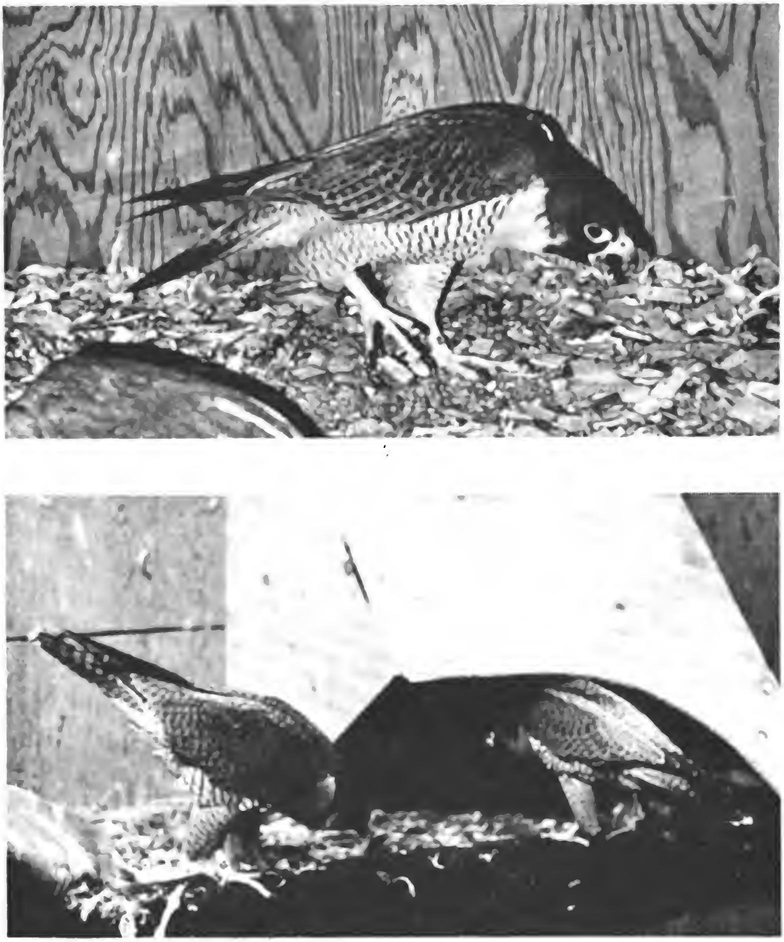
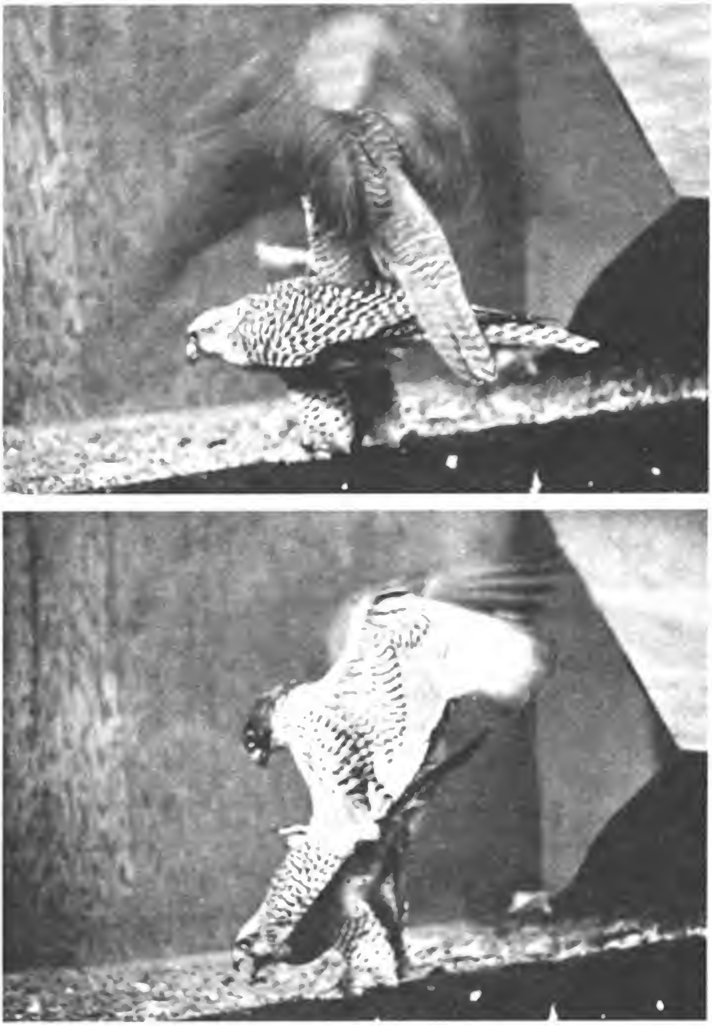
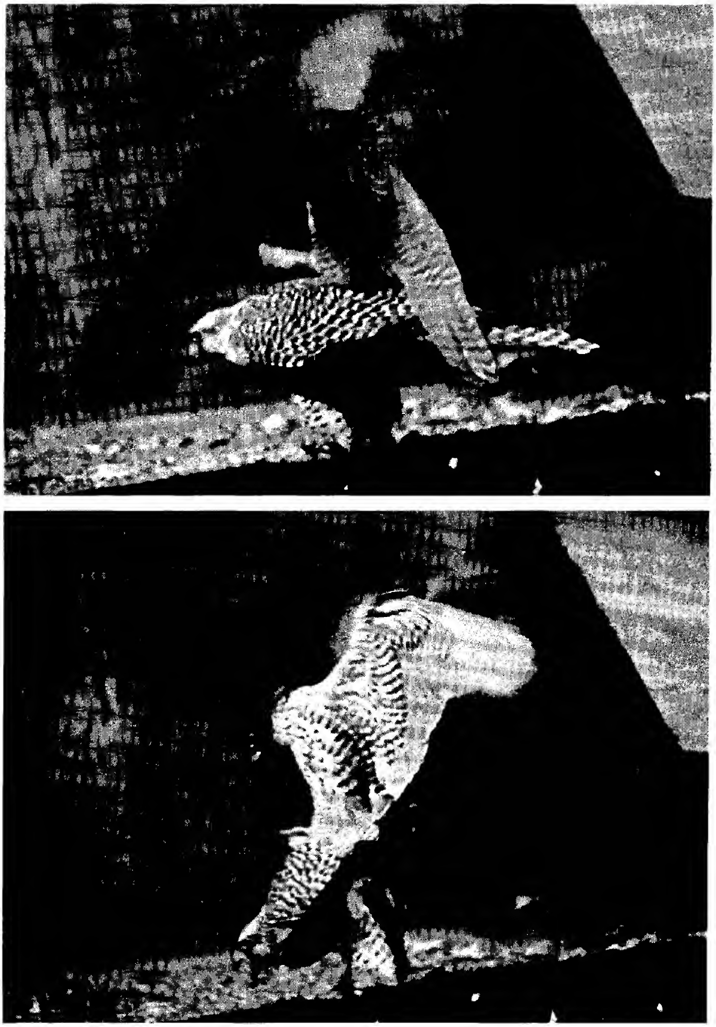


Figure 1. Courtship postures common to four species of large falcons. (a) Male Peregrine approaching the scrape in a Horizontal Head-Low Bow. (b) Peregrines during a partly aggressive interaction; female on left in Extreme Head-Low Bow; male in a transitional posture showing some aspects of the Hitched-Wing Display.



(e) Gyrfalcons as the male flies to mount; female in Copulation Solicitation posture.
(f) Gyrfalcon copulation; male in Curve-Neck posture.



(e) Gyrfalcons as the male flies to mount; female in Copulation Solicitation posture.
(f) Gyrfalcon copulation; male in Curve-Neck posture.

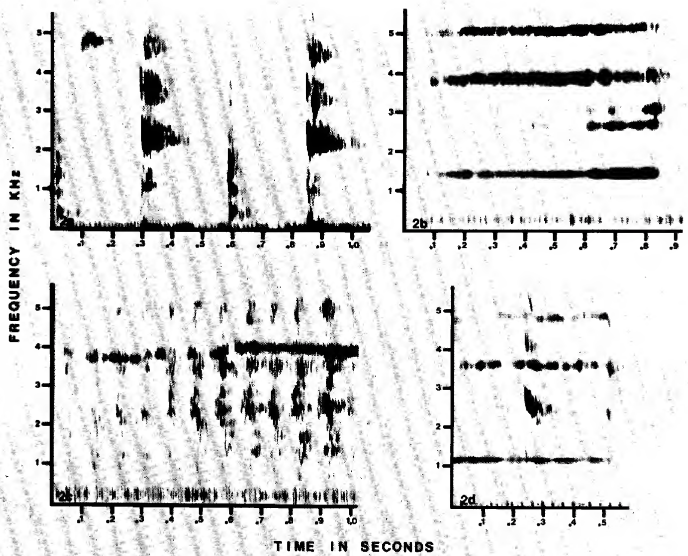


Figure 2. Peregrine Falcon vocalizations. (a) Eechip (two units) given by either sex during Ledge Displays, Food-Transferring, contact vocalizing, aggressive interactions, by male during copulation (phonetics in figure: ku ee chip, ku chip). (b) Wail (one unit) given by either sex when motivated to change the social context. (c) Chitter (segment only) given by either sex, especially by the male during aggressive interactions, precopulatory behavior, and during copulation (horizontal band at 3.9-4.0 KHz is a female Whine used here to solicit copulation). (d) Copulation Wail (segment only) given by the female during copulation (burst at 0.25 sec. is part of male vocalization).

especially by the female, and nibbling between beaks. The female's head is usually very low with her beak directed upward, while the male faces downward. If billing occurs during a Mutual Ledge Display, the normally loud Eechip vocalization tends to diminish toward Peeping and quiet female Chupping–incomplete variations of the Eechip sound unit.

5. *Scraping*. Scraping is exhibited by either sex during solitary activity on a ledge or as part of an Individual Ledge Display. There is some question as to whether the behavior should be considered a component of Display. During scraping the body is canted forward, weight on the breast, beak frequently in the substrate, the tail relaxed and sloping toward the ledge. A shallow depression, the scrape, is made by vigorous backward pushing with the feet. This behavior often occurs in a series with a shift in position between bouts of scraping. No vocalization accompanies this behavior. With the exception of females from about five days before laying, no "rocking" movement is made before settling on the breast. The rocking behavior always occurs as a falcon settles onto eggs for incubation and has been described in detail by Nelson (1970) for wild falcons. The behavior in captive birds is identical.

6. *Food-Transfer Display*. A common courtship Display involves the transfer of food from one mate to the other, usually male to female. Either sex may initiate a transfer. The female uses a Wail vocalization or rarely a Whine, combined with a vertical head-low posture to solicit transfers when the male does not have food. If the male has food, the Wail and Eechip vocalizations are used about equally by the female, often accompanied by the Vertical Head-Low Bow Display.

Male solicitation, which elicits the female's approach, always occurs when he has food, either spontaneously or initiated by female intention movements to engage in transfer. This solicitation by the male is characterized by a very sharp and clear Eechip vocalization. The male alternates between a relaxed posture, with the head up, and a posture with his head down while he manipulates or contacts the prey item. This posture, with the head low, does not appear to be the nonaggressive Head-Low Bow Display. Transfer from the female to the male is not obviously solicited.

Prior to actual transfer, the male picks the prey item up in his beak and stands vertically, head up. The female maintains head-low postures, often horizontal, and both sexes give complete Eechip vocalizations. Nelson and Campbell (1974) have described variations on the actual transfer sequence and behavior associated with incomplete Displays.

7. *Hitched-Wing Display*. Engaged in by both sexes, this Display is especially characteristic of the male throughout the reproductive cycle, developing as sexual motivation reaches its peak (Weaver and Cade 1974). It is consistently given in flight to and from copulation and during male precopulatory behavior. This Display can be divided into two forms, flying and standing (figs. 1c and 1d). The latter is probably the same behavior as the Slow Landing Display described by Nelson and Campbell (1973, 1974).

During Hitched-Wing flight the wings are held high, with short wing-beats mostly from the wrist. The legs are well forward, and the tail is depressed resulting in a slow-motion, bouncing flight. Frequently the flight path involves low approach to the perch with a last-minute bound above and then straight down onto the perch. No bounce occurs when the male flies to mount for copulation.

Standing Hitched-Wing Displays occur briefly to moderately long (2 seconds) after the male lands on a perch, frequently in the context of Mutual Ledge Displays. It is always expressed prior to copulation. Most often the body posture is vertical to semihorizontal, high on stiff legs. The head is low, and the wings are hitched up high against the body to form a deep, V-shaped depression along the back. Another variation includes a horizontal head-low position, legs stiff and wings hitched.

The male precopulatory posture is especially interesting in its combination of the sexually motivated Hitched-Wing Display and components of the Agonistic Head-Low Bow. The body is vertical, wings hitched and legs stiff. The head is lower than the shoulders with beak directed at the female, which is usually soliciting copulation (see below). Vigorous bowing, frequently with a side-to-side swing, is part of this Display. The Chitter is a frequent male vocalization during precopulatory behavior.

8. *Copulation Solicitation Display.* The female's motivation to copulate is communicated by a series of postures and vocalizations, partially described by Nelson and Campbell (1973). Solicitation may begin with the Whine vocalization, concurrent with or just preceding a Vertical Head-Low Bow. This is usually given when the male is at some distance. Primary solicitation will follow if the male shows reaction. During primary solicitation, either following the vertical solicitation just described or independently, the female assumes a horizontal head-low posture. Again the Whine vocalization is given, the tail is close to horizontal, panel feathers are raised, and her orientation is usually perpendicular to the male. This phase of the Copulation Solicitation Display may continue for up to 30 seconds. Just as the male shows intention to mount, the female sleeks her panel feathers, crouches and leans forward slightly, and sometimes begins to move her tail up and to the side in preparation for copulation.

9. *Copulation.* During copulation the female is pitched forward, making an angle of about 45° with respect to the perch. The Copulation Wail is given throughout (fig. 2d). As the male mounts, the female spreads her wings out at the elbow about one-fourth open. The tail, up and to the side, may be partly spread.

The male flaps his wings throughout copulation, maintaining an upright posture with the neck extended and bent in a curve (fig. 1f). Usually the male gives one or two bursts of the Chitter vocalization just before, during, and/or just after mounting, and then Eechips sporadically. Some individuals give bursts of Chitter throughout. Toward the end of copulation the male stops his tail movements, pressing his cloaca against the female's. Rapid wing-beats accompany this tail-press. The female may spread her tail partly at this time, and the male departs with a Hitched-Wing Display directly afterwards.

10. *Threat Behavior.* The two major Displays have been described by Nelson and Campbell (1973). The characteristic posture for Horizontal Threat is with tail, body, and head all in a horizontal plane. The beak is directed at the mate, wings slightly extended, head and body feathers erect. In Upright Threat, the body is vertical with most feathers erect. The tail and wings may be spread to varying degrees; the beak is usually open.

Comparison of Peregrine and Gyrfalcon Courtship Behavior

We present here details of only those aspects of Gyrfalcon behavior that differ from the Peregrine behavior already described. Most of the courtship Displays and behavior patterns of these two species are very similar and can be designated by the same names. Unless otherwise stated, components of the various behavior patterns in both species are typified by the description for Peregrine Falcons in the previous section.

1. *Head-Low Postures.* Head-Low postures are exhibited by both species in quite similar contexts. Gyrfalcons show Horizontal and Vertical Head-Low Bow Displays, and use head-low postures during all Ledge Displays and Food-Transferring. As in the case of Peregrines, the accompanying vocalizations are somewhat variable; most often a Whine or brief Chitter is given for the Bow Displays, and Chupping occurs during Ledge Displays and Food-Transferring (fig. 3).

The frequency with which these Displays and postures are exhibited is the major difference between the two species. In Gyrfalcons there is very little intermediate variation be-

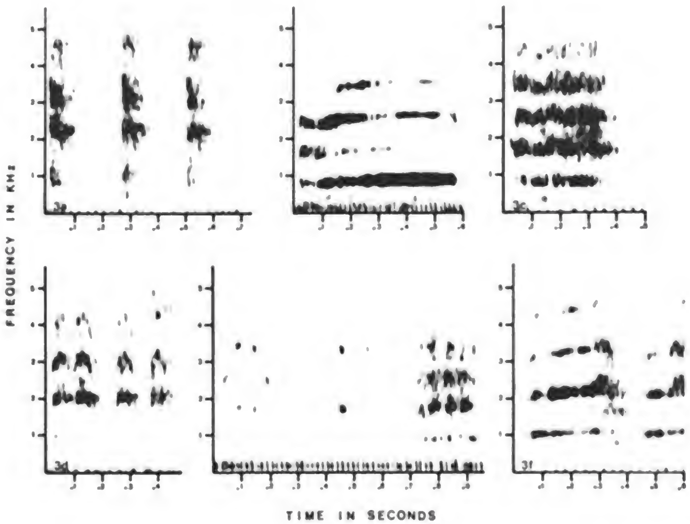


Figure 3. Gyrfalcon vocalizations. (a) Chup (three units) given by either sex during Ledge Displays, Food-Transferring, contact vocalizing. (b) Wail (one unit) given by either sex when motivated to change the social context. (c) Chitter (one burst) given by either sex during aggressive situations, by male before copulation, and probably by male during copulation. (d) Chatter (four units) given by either sex, especially by the female during Mutual Ledge Displays and Food-Transferring. (e) Copulation Solicitation (segment only) given by the female; first 0.6 sec. in figure is the Whine of initial solicitation followed by the first burst of primary solicitation. (f) Copulation Wail (segment only) given by the female during copulation (smudge at 0.3-0.4 sec. is the male vocalization).

tween the vertical and horizontal forms of the head-low postures. The threshold for assuming the more intense horizontal head-low posture is high in male Gyrfalcons, and females use the Head-Low Bow Display much less frequently than Peregrine females. Neither sex of Gyrfalcon shows the vigorous bowing so conspicuous in Peregrines. One of the most frequent contexts eliciting Head-Low Bow Displays in Peregrines is the approach of the mate or intention movements of approach. Use of the Display in this context was more frequent for males than for females in both species. The Gyrfalcons were less intense about the interaction, and intention movements rarely elicited display. Frequently the male did not display until the female was actually landing on his perch.

In our Gyrfalcon pairs there was no behavior pattern strictly parallel to the Agonistic Head-Low Bow observed in Peregrines. Female Copulation Solicitation has some characteristics in common with the Agonistic Bow, but, in general, orientation away from the male is necessary for mounting. Behavior comparable to the Extreme Head-Low Bow was not observed in the Gyrfalcons.

2. *Individual Ledge Displays*. The contexts in which these Displays occur are identical in both species. Visual contact with the mate is very important, reaction of the mate being a determinant of the Display intensity and duration.

The Male Ledge Displays of Gyrfalcons are nearly identical to those of Peregrines. The vocalization in Gyrfalcons is always a complete Chup as compared with a tendency of the Peregrine vocalization to degenerate. The reason may be that the basic Gyrfalcon vocal unit is a single syllable, whereas the Peregrine's is complex. There is a possibility that Male Ledge Displays are more frequent and more vocal in Gyrfalcons, but the sample size is too small to be certain.

Female Ledge Displays in both species show similar differences from Male Ledge Displays. These include less well-defined postures and a marked tendency to change into non-communicative activity. The female Gyrfalcon may more consistently maintain a head-low posture early in the Display.

3. *Mutual Ledge Display*. Although the functions and general characteristics of the Mutual Ledge Display are similar in Peregrines and Gyrfalcons, differences in movement, duration, and vocalization are conspicuous. In both species the Display is primarily organized around a potential nest-scrape and is frequently preceded by a Male Ledge Display. In Peregrines as well as Gyrfalcons, as the Mutual Display begins, both sexes are in a horizontal head-low posture.

In Peregrine Falcons there is considerable movement by one or both sexes around the scrape as well as pauses in the Display followed by renewed vigorous activity. In some Peregrine pairs the female is as likely as the male to terminate the Display by leaving the scrape. By contrast, Gyrfalcons tend to maintain stationary positions during the Mutual Ledge Display and rarely pause. It was extremely rare for our female Gyrfalcon to terminate a Mutual Display. Our male Gyrfalcon usually terminated the interaction after only five to ten seconds, resulting in Display durations shorter than was usual in Peregrines.

The greatest apparent difference between the vocalizations of Gyrfalcons and Peregrines is change in repetitiveness of vocalizations during the Display, rather than the obvious differences in the basic sound units. Male and female Peregrines give an Eechip vocalization with some variability depending on the intensity. In addition, Peregrines show considerable variability in the regularity with which successive units of the vocalizations are given. By contrast, male Gyrfalcons give very regular Chup vocalizations throughout the Display. In the female Gyrfalcon there is always a distinct change in vocalization as the male leaves her alone at the nest-scrape. During most of the interaction she gives a series of very fast Chup

units, but these increase in speed to a Chatter as the male departs (fig. 3d). When the female of either species remains in the scrape after the male has gone, vocalization diminishes, becoming sporadic, soft, and, in Peregrines, incomplete. The Gyrfalcons gave Mutual Ledge Displays only at the nest-scrape. Peregrines occasionally exhibited identical interactions at other locations, especially early in the courtship period. Billing was not observed during courtship in the successful pair of Gyrfalcons, but it has been seen in other pairs.

4. *Scraping.* The major characteristics of this behavior pattern are identical in the two species. The conspicuous "rocking" movement of Peregrines as they settle on eggs (Nelson 1970) are present in most scraping bouts by captive Gyrfalcons. This movement was observed in males and females beginning in January, when scraping activity first began. It was observed during Peregrine courtship only as the female did it a few days before laying.

5. *Food-Transferring.* The behavior patterns that comprise Food-Transferring are very different in Peregrines and Gyrfalcons although the function of the Display appears to be the same in both species. It is an important courtship interaction, expressed somewhat more frequently in the captive Gyrfalcons than in the Peregrines. The frequency of female-to-male transfer was low in both species, but unlike Peregrines the male Gyrfalcon rarely took food to the female's perch for transferring. It was more usual for him to prolong solicitation, waiting for the female to approach for the transfer.

Comparisons of vocalization are similar to those of the Mutual Ledge Display. Both sexes of Peregrine give a complete Eechip vocalization, and the male gives especially clear and sharp Eechips when soliciting a transfer. Gyrfalcons give Chup vocalizations through most of the interaction. The female increases the speed of repetition to a Chatter as the transfer occurs.

The postures of both sexes are different in the two species. In contrast to the upright posture of a male Peregrine, the male Gyrfalcon maintains a vertical to horizontal Head-Low Bow while soliciting a Food-Transfer. The male Gyrfalcon occasionally looks up at the female during solicitation, but on her approach he picks up the food in his beak and maintains a head-low posture until the transfer is complete or the female loses interest. Female Gyrfalcons approach in an entirely horizontal posture or slightly head-low. This mildly aggressive posture is maintained during the actual transfer and contrasts with the conspicuous head-low posture of female Peregrines throughout the Food-Transfer sequence. Males of both species tend to leave the area of transfer immediately after the interaction is complete, but the tendency is particularly pronounced in Gyrfalcons. Food-Transfer solicitation by the female is similar in the two species. As is usual, the Gyrfalcons tend to be more vocal, including a nearly continual vocal response by the female from the onset of male solicitation until the actual transfer.

6. *Male Precopulatory Display*. Male Peregrines and Gyrfalcons have distinctive postures used during precopulatory sequences. These are the Hitched-Wing and Curve-Neck Displays, respectively. The frequency with which these Displays appear is very different in the two species. The Hitched-Wing Display is first seen early in courtship and appears to function as a general signal. In Gyrfalcons the Curve-Neck Display was observed only when the male was motivated to copulate or just prior to a copulation attempt. Because of this specialized use of the Curve-Neck Display in Gyrfalcons, it always elicited some female response.

A close comparison is possible between Peregrine precopulatory Hitched-Wing Display and Gyrfalcon Curve-Neck Display. During these Displays the body is drawn up to maximum height, and the plumage is sleeked. Gyrfalcons direct the beak away from the female, and Peregrines often direct the beak toward the female. Body postures accentuate the head position in both species. Gyrfalcons extend and bend the neck into an inverted U shape;

Peregrines have their wings hitched over their backs, accentuating the head-low posture. When the female is very close, nonaggressive postures are added to or replace the above postures, at least in Gyrfalcons. Male Gyrfalcons either assume a head-low vertical posture at high intensities, or turn perpendicularly to the female, maintaining the Curve-Neck Display. When in close proximity to the female, male Peregrines present a profile, although the body may still be oriented toward the female. At higher intensities male Peregrines will frequently drop to a horizontal body posture, with Hitched-Wing and the Agonistic Head-Low position.

Males of both species use vocalizations during these Displays that are also used during clearly aggressive interactions. The male Peregrine frequently emits the Chitter vocalization (described by Cade 1960, Nelson 1970) just prior to mounting attempts. This vocalization has also been heard when the female was trying to pull food away, during exchanges for incubation, and while in Horizontal and Upright Threat. Male Gyrfalcon vocalizations just prior to mounting were difficult to resolve behind the overriding vocalization of the female. Recorded segments that have been analyzed appear similar to the agonistic vocalizations given during Horizontal and Upright Threat.

7. *Copulation Solicitation*. Some postural aspects of female Solicitation for Copulation differ between species, but the Display is similar in its progression and vocal characteristics. Generally there seems to be more of an agonistic component to Gyrfalcon solicitation. Although both females posture horizontally during primary solicitation, the female Gyrfalcon often approaches head-on in an entirely horizontal posture (i.e., components of horizontal threatening, fig. 1e), and the Peregrine female is stationary, usually oriented either perpendicular to or away from the male. Female solicitation in Peregrines is distinctly head-low. The female Gyrfalcon does turn perpendicularly when close to the male, and copulation proceeded in our pair when this orientation was maintained. In both species an initial solicitation was sometimes made from a vertical head-low posture, usually at some distance from the male.

8. *Copulation*. Female Peregrines and Gyrfalcons have distinctive Wail vocalizations given only during copulation. Their bodies are tipped forward to an angle of 45°, legs stiff and head in the body plane. The vocalization emitted by the male is variable even for an individual, but is usually given in bursts. This vocalization in Gyrfalcons appears to be the same as during the precopulatory sequence, although clear sonographs could not be made. The copulation posture of males is identical in Gyrfalcons and Peregrines. It is a vertical posture with the Curve-Neck head position (fig. 1f). In Peregrines, at least, the talons are balled up into a loose fist, weight on the tarsi (Nelson 1970; see also Mueller 1970). The talon position is difficult to see in Gyrfalcons owing to the dense plumage, but they appear to be balled up also; sometimes the male's hallux appears to be locked under the female's humerus.

9. *Aggressive Behavior*. The behaviors in this category are similar in the two species. Well-adjusted pairs rarely showed any agonistic behavior, and Upright Threat was not observed except in new and/or incompatible pairs.

Comments on the Courtship Behavior of Lanner and Prairie Falcons

Although Lanner and Prairie Falcons have not been subjected to the same detailed observation as our Peregrines and Gyrfalcons, we have enough incidental observations to know that all basic Displays discussed in the previous section are used by these species too. In most cases the forms of their Displays and vocalizations bear striking resemblances to those of Gyrfalcons and serve further to emphasize the close phylogenetic ties among these forms,

which are usually allied in a separate subgenus from the Peregrine. The displays and vocalizations of Prairie Falcons and, in particular, Lanners are more subdued and less conspicuous than the vigorous and loud displays of the Gyrfalcons, but otherwise there are few qualitative differences. One exception is the Chupping call of the Prairie Falcon, which is more similar to the Peregrine's "Eechip" than to the Gyrfalcon's "Chup" (fig. 4a). The Curve-Neck Displays of the males of all three species prior to copulation are strikingly sinilar and stand in maked contrast to the Hitched-Wing Display of the male Peregrine. One characteristic of Prairie Falcons that is different from the others is the high degree of female aggression, which often erupts into overt attack on the male during the early stages of pairing. As a consequence, Head-Low Bows and other forms of agonistic display occur more frequently and occupy a greater portion of the total courting period than in the case of the other species.

Seasonal Ontogeny of Reproductive Behavior

Owing to the individual variability in seasonal development and the small sample of paired Gyrfalcons, this discussion of seasonal ontogeny is limited to Peregrines.

Initial courtship interactions were observed earlier in each successive year of breeding for at least the first three years. Egg-laying also tended to begin somewhat earlier although the courtship period still lengthened each year. The earlier onset of copulation with respect to laying dates was especially consistent; all pairs showed this progression (table 1). There is some evidence to suggest that the seasonal ontogeny of behavior becomes stabilized after several years. The three experienced pairs (two breeding for the third time, one for the third and fourth times) showed striking similarities in courtship development. All pairs initiated courtship at about the same time, began copulation within one week of each other, and began to lay eggs within a period of ten days. The development of courtship outlined below uses the temporal progression characteristic of the pairs in their third or fourth breeding season (fig. 5). The actual dates used in this section are specific to our particular environmental conditions. They are expected to vary depending on local weather conditions, latitude, and photoperiod manipulation.

A gradual increase in activity on the nest-ledge by both sexes is the first indication that courtship is beginning. Ledge behavior is most conspicuous in the male, beginning in early January. He displays at several scrapes, often on more than one ledge. This pattern of maintaining a number of scrapes is exaggerated in the young pairs breeding for the first time. During this early period both sexes frequently use Head-Low Bow Displays or Mild Threat when approached closely or suddenly.

Toward the end of January, Mutual Ledge Displays and Food-Transferring begin to develop simultaneously. The female shows interest in Male Ledge Displays and also hesitates before getting food when it is first introduced. This hesitation permits the male initial access to the prey (see Willoughby and Cade 1964). Solicitation for Food-Transferring is displayed repeatedly by the male although if the female approaches, he tends to move away, resuming solicitation from a new perch.

Male Hitched-Wing flying becomes apparent about one month after the onset of courtship. For an additional two or more weeks the female responds directly to male Hitched-Wing flights over her or close by. This reaction is usually the Vertical Head-Low Bow accompanied by either Eechip or sometimes the Whine vocalization. Apparently the female becomes habituated to these Displays, as the male uses Hitched-Wing Displays for almost all

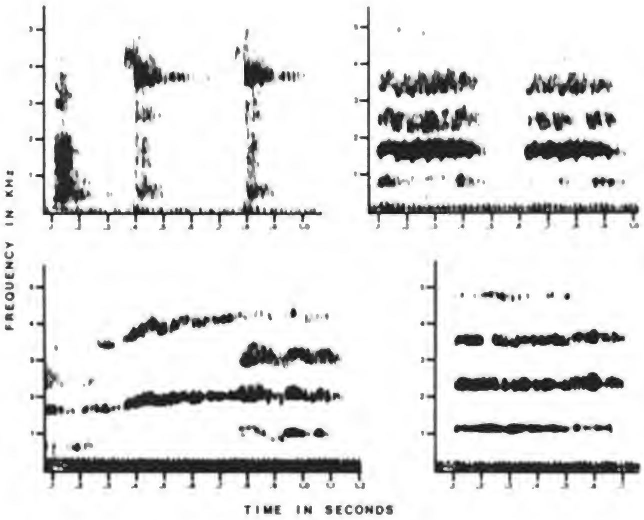


Figure 4. Prairie Falcon vocalizations. (a) Kuduchip (two units) given by either sex during Ledge Displays, Food-Transferring, contact vocalizing, aggressive interactions, and rarely by male during copulation (phonetics in figure: kudu chip, chip). (b) Chitter (two bursts) given by either sex during aggressive interactions. (c) Copulation Solicitation Whine (segment only) given by the female. (d) Copulation Wail (one unit) given by the female during copulation.

Table 1

The relationship of breeding experience to the start of copulation during courtship.

Subspecies and year of breeding	Date of first observed copulation	Days prior to first egg
F. p. tundrius		
pair CC:		
first year (1972)	April 10	2
third year (1974)	March 5	15
fourth year (1975)	March 3	23
pair CH:		
first year (1973)	April 8	5
second year (1974)	March 7	10
third year (1975)	February 26	24
pair U8:		
first year (1975)	May 16	0
*F. p. pealei**		
pair MP:		
first year (1973)	April 1	2
second year (1974)	March 22	4
third year (1975)	March 3	15

* This pair bred successfully for two years before 1973 at another breeding facility.

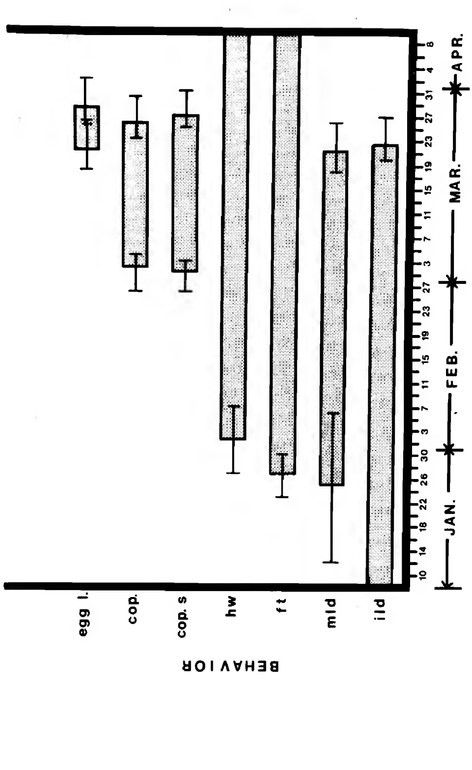


Figure 5. Seasonal ontogeny of Peregrine Falcon courtship (third or fourth year of breeding). Shaded bars represent the duration of behavior from the mean beginning date to the mean ending date; ranges are indicated. Behaviors: Individual Ledge Display (ild), Mutual Ledge Display (mld), Food-Transferring (ft), male Hitched-Wing Display (hw), female Copulation Solicitation (cop. s), Copulation (cop.) and egg laying (egg l.) (Based on three pairs breeding in 1975 (two *F. p. tundrius* and one *F. p. pealei*) plus one of the same *F. p. tundrius* in 1974.)

movements across the room, until the end of incubation. Young males are not as consistent in using the Hitched-Wing Display. Female reaction to this activity steadily decreases, and late in the courtship period her reaction initiates steps toward Copulation Solicitation. The Whine vocalization is almost always used in these situations.

For a period of about three weeks in February, Mutual Ledge Displays and Food-Transferring develop into frequent interactions, and Head-Low Bow Displays become less frequent. Mating behavior, including female solicitation for copulation and male precopulatury posturing, is first observed in late February to early March, about eight weeks after the onset of courtship. The females perform Copulation Solicitation Displays for a variable length of time before the males complete the sequence by mounting, usually in less than two days. In all cases the early mating behavior was identical to the precopulatory sequences observed later in the year. These involve female Copulation Solicitation with bowing, alternating with the male Vertical Head-Low Bow or, more often, the precopulatory Hitched-Wing. In both sexes the bowing is vigorous: a fast, jerky movement to the bow position, then up to the starting posture.

Initial Copulation Solicitation is observed about three weeks before laying. At first many copulation sequences are incomplete, and successful copulations are short, averaging five to six seconds depending on the pair. Two to three weeks before laying, copulation is already a regular interaction, with a duration of eight to ten seconds, occurring at a frequency of two to three copulations per hour during the most active period (first hour of light). One week before laying, copulation increases to a frequency of three to four per hour during the first hour of light. Copulation continues in most pairs until the third egg is laid. Although copulation was not observed in some pairs after the second egg was laid and very few pairs copulated after the third egg, full clutches were consistently fertile. A sudden increase in the frequency of copulation occurred on the day that the second egg was laid, either a few hours prior to, or after, laying.

The male shows little motivation to incubate the first egg and tends to continue Male Ledge Displays around the egg, sometimes moving the egg out of the nest-scrape and then displaying in the empty space. The female incubates immediately if weather conditions require it although more often she only stands over the egg and does not begin continual incubation until the second or third egg.

Discussion

1. *Limitations of Studying Captives.* When behavioral data are based on the study of captive animals, extreme caution is necessary in extending conclusions to include wild situations or even other captive environments. In addition to other factors, the frequency with which certain behavior patterns occur can be very different in captive animals. There is also the temptation to consider as normal the behavior of captive animals that successfully reproduce. Such an assumption can be misleading. Highly unnatural pair-bonds and behavioral development may still result in fertilization, as in the case of interspecific crosses (e.g., Morris and Stevens 1971).

One factor that might contribute to such abnormality is the stimulus-deprived environment experienced by captive animals and the resultant responsiveness to suboptimal stimuli. A second bias may come from exaggeration of individual differences in behavior. Enforced pairing and limited or incomplete environments accentuate individual variations in behavior

that may or may not be significant in nature. Evaluating the importance of these behavioral differences can be helped by determining the causes of their expression in the captive situation.

The interpretation of behavior in captivity is dependent on study of the same behavior in nature, not vice versa. The only exception might be studies of organisms for which the entire range of environments experienced by the species within the cycle of behavior under study can be contained or accurately simulated in the study chamber.

The captive environment of our falcons cannot satisfy these requirements. The breeding chambers provide a minimal environment, satisfactory in that successful breeding can occur. The behavior of wild North American species of *Falco* has been studied to varying degrees. Peregrine Falcons, Prairie Falcons, and the American Kestrel (*Falco sparverius*) are best known, and the behavior of Gyrfalcons is just beginning to be described. Very little is known of the Lanner Falcon. Most of these studies include only incidental behavioral observations. A few have considered in more detail the repertoire and temporal patterning of reproductive behavior (e.g., for American Kestrels, Cade 1955; for Peregrines, Fischer 1968, Nelson 1970, Fyfe 1972, Wrege unpubl.; for Gyrfalcons, Platt 1976). Thus a small literature exists with which to gauge the behavior patterns of captive falcons.

Several basic differences are apparent when comparing the behavior of captive falcons with what is known of their behavior in the wild. The close proximity of the captive pair and the limited space have resulted in an emphasis on certain Displays, while others are deleted from the repertoire. Food-Transferring and especially Ledge Displays are much more frequent in captive Peregrines—probably because of the almost constantly available stimuli that elicit the behavior patterns. It is likely that other behaviors vary considerably in frequency when compared to wild falcons. Some courtship Displays observed in nature require considerable space, such as, territorial flight Displays, mutual defense Displays, and others (see Cade 1960, Nelson 1970). These behavior patterns are not observed in captivity, although some others may be modifications of them.

The contextual use of certain vocalizations is different in captive and wild falcons. Evidence suggests that many vocalizations of falcons communicate intensity of motivation, as opposed to direction of motivation to perform a specific action. The degree to which this might be true in wild falcons has not been determined. The close proximity of mates in captivity makes unnecessary vocalizations that may function in the wild as long-distance signals, and another vocalization is substituted (Platt pers. comm., Wrege unpubl.) For example, a wild male Peregrine will often solicit Food-Transferring with a Wail vocalization as he returns to the eyrie site. As the female approaches for the transfer, he begins to Eechip. In captivity the male solicits a transfer only with the Eechip vocalization, which continues until the Display is complete.

Individual behavioral characteristics of captive falcons greatly influence reproductive success. Continued close proximity and the difficulty of avoiding interactions are probably contributing factors. Observations of wild Peregrines and Gyrfalcons indicate that males may spend considerable time away from the females, either hunting or perching out of sight. No data are available to determine whether individual differences in behavior affect choice of mate and breeding success in wild falcons, but such influence seems likely (Cade 1960).

2. *The Function of Displays in Pair-Formation and Pair-Bonding*. The Displays and vocalizations of Peregrines, Gyrfalcons, Prairie Falcons, and Lanner Falcons can be divided roughly into three groups. First, nonaggressive behavior patterns include the following: All the head-low postures; Head-Low Bow Displays (excluding the agonistic form); Ledge Displays; Food-Transferring; Copulation Solicitation Whine; the Eechip vocalization and Ex-

treme Head-Low Bow in Peregrines; Chup and Chatter vocalizations in Gyrfalcons; Kuduchip in Prairie Falcons; and similar vocalizations in Lanner Falcons. These behaviors can be further subdivided into anti-aggressive or appeasement and approach-eliciting behaviors, according to the type of interaction. The uses of nonaggressive displays in these two forms are discussed in the section on the pair-bond and female dominance.

A second group of behavior patterns includes the male precopulatory postures in each species, female Copulation Solicitation in Gyrfalcons, and the Wail vocalizations in each species. It is difficult to label these behaviors as either aggressive or nonaggressive. In each case there appear to be aggressive components.

Finally, the remaining behavior patterns can be grouped as at least partly aggressive. These are the Agonistic Head-Low Bow Displays in Peregrines, any all-horizontal posture, Chitter vocalizations, and the Upright and Horizontal Threat Displays. Of course, none of the three groups of behavior patterns is rigid. In each species (and in some more than others) postures and especially vocalizations tend to intergrade depending upon changes in motivation.

Many courtship displays in falcons appear to integrate the pair and to ease co-inhabitation of a limited space. The effectiveness of a display and its frequency are probably related to the degree of sexual readiness of the mates. Male Ledge Displays stimulate reproductive behavior in females and initiate pair integration. Mutual Ledge Displays, Billing, and Food-Transferring all result in close, nonaggressive interactions. This does not imply that aggression and fear are never seen as part of the Displays; rather, it means that the outcome of the interaction is nonaggressive and helps to form a pair-bond.

Studies of captive and wild Kestrels suggest that copulation may function in pair integration very early in the reproductive season (Willoughby and Cade 1964). Fischer (1968) mentions copulation as the first interaction of the season in some wild Peregrine pairs, and Fyfe (1972) has described copulation in Prairie Falcons on the first day the pair was together at the eyrie. This association of copulation and initial pair-bonding was not observed in the four captive species of *Falco* studied here. Established pairs initiated copulation very early relative to egg-laying, but all other courtship patterns were well established at the time of first copulation. This pattern of pair-bond initiation, involving considerable courtship activity preceding first copulation, was also observed in captive Peregrines introduced to one another abruptly at the start of the breeding season (Nelson and Campbell 1973, 1974). Nonetheless, copulation probably does function importantly in strengthening the pair-bond. Copulation in the Gyrfalcon pair continued for 39 days before egg-laying, progressing from very short attempts that were terminated by female aggression through full-length copulations beginning 20 days before laying.

The Displays in each species of *Falco* can be characterized by the same name and include very similar postures, with the exception of the Hitched-Wing and Curve-Neck male precopulatory Displays. This likeness is suggestive of a similarity in function as well. Without the analysis of quantitative data, it is difficult to determine whether important interspecific differences exist in the function of various Displays in pair-bonding and integration. At this time, differences are not apparent, even when comparing the phylogenetic group of Gyrfalcons, Prairie Falcons, and Lanner Falcons to Peregrine Falcons. The major differences in behavior patterns are of frequency, intensity, and mate response. These differences, which may be intraspecific as well as interspecific, appear related to the nature of the pair-bond, especially the dominance relationship between the sexes.

3. *The Pair-Bond and Female Dominance*. The relationship of male and female in the pair-bond of falcons has been interpreted in different ways. In most cases, the interpretation

has been incidental to an explanation of reversed sexual size dimorphism, and this may account for the lack of data specifically bearing on the relationship. The following discussion about the pair relationship in captive falcons does not depend on any theory concerning the evolutionary pressures causing size dimorphism. Hagen (1942) suggested that female dominance was necessary to avoid filicidal behavior by the male. In most species of falcon, the male participates to some degree in incubation and care of the young. There is little evidence to suggest that a real threat exists, and strong selective pressure to eliminate such a tendency in the male's behavior would be expected. Cade (1960) placed importance on the division of labor that is very common in *Falco*, suggesting that female dominance might be necessary to maintain the male in his role as food provider. Amadon (1975) speculated that female raptors may be "more submissive or passive" relative to the male, at least during the initial pair interactions. To date there has been virtually no study of these initial interactions in any raptor. A different interpretation of the pair-bond resulted from the study of *pealei* in the Queen Charlotte Islands by Nelson (1970). He suggested that dominance was related to the location of the interaction, with the male being dominant in aerial encounters where his agility would be an advantage, and the female being dominant on the nest-ledge and during other close interactions where her size would be favorable. Observations on a captive pair of Arctic Peregrines led to the interpretation that the male dominated the female in the breeding chamber (Nelson and Campbell 1973).

There has been too little detailed behavioral analysis of wild falcons to determine the dominance relationship during reproduction. Our observations of four species of captive falcons indicate that the female is dominant in all species and in pairs that breed successfully. Unsuccessful breeding can often be correlated with either very dominant females, inhibiting almost any mutual behavior; with a lack of dominance by either sex; or, exceptionally, with a domineering male.

The relative frequency of aggressive and nonaggressive postures in each sex may be used as an indicator of the pair relationship. The use of these postures within ritualized courtship Displays as well as independently is important, and frequencies appear predictable on the basis of the degree of size dimorphism exhibited in the pair. A specific value for the relationship between size dimorphism and the relative frequencies of these behaviors would not be found in most captive falcons, for the following reasons. Differences in the history of each bird, primarily in its handling by humans and experience with conspecifics, result in a large variation in aggressiveness that influences the frequency of aggressive and nonaggressive behavior. We do feel, however, that a general pattern is demonstrable.

The Peregrine is the most dimorphic of the species studied and has been observed more intensively than the others. Possibly the most conspicuous behavior pattern throughout the reproductive season is the Head-Low Bow. Both sexes exhibit this Display, and intergradation is nearly continuous between the less intense vertical form and the extreme horizontal form. In most cases this Display appears to be anti-aggressive in meaning, rather than approach-eliciting. This distinction is important. An anti-aggressive posture is clearly one that inhibits aggression. Approach-eliciting postures signal the absence of aggressive motivation in the sender. It is quite possible for the same posture to take on either meaning, even when given by the same individual. The meaning depends on the relative dominance of the interacting animals in the context of that interaction or in anticipation of the interaction. The problem comes in deciding which meaning a given posture has and in trying to avoid shaping the decision on the basis of preconceptions. We would like to stress that all these comparisons are of relative frequencies. It is quite evident that each bird is intimidating to the other,

and both sexes must use postures that can be interpreted as anti-aggressive and as approach-eliciting.

The male Peregrine exhibits head-low posturing much more frequently than the female, often responding to female movements at a considerable distance. Female intention movements to approach the male elicit postures close to horizontal, and approach by the female frequently causes displacement of the male to another perch. Although the female also exhibits these postures, vertical positions predominate. Female displacement on male approach is not frequent.

In well-adjusted pairs, the very aggressive Upright and Horizontal Threat postures are rarely observed as interactions between the mates. With new pairs these displays may occur early in the season, but are observed less frequently as the pair-bond develops. Although the female may approach the scrape in an all-horizontal posture during a Mutual Ledge Display, she immediately assumes a head-low posture if the male looks up. It is unlikely that the horizontal posture in this case is really aggressive. Entirely horizontal approach to the scrape is usual in both sexes prior to Individual Ledge Displays–probably a relaxed posture for walking on a ledge or the ground. It is significant that the female's posture changes when the male looks at her; this is not seen in Gyrfalcons during some interactions (see below).

Postures and vocalizations that are apparently aggressive occur regularly in the copulation sequence of Peregrines. The female posture at this time is totally nonaggressive, as is her Whine vocalization. The male uses the Chitter vocalization and postures with aggressive components. There is little doubt of the aggressiveness of the Chitter, at least in some contexts. It has been observed during Upright Threat encounters, during forced (by female) Food-Transferring, and by both sexes when trying to force the mate off the eggs. The combination of this vocalization with the partly aggressive postures just before mounting is difficult to interpret. The female is not always intimidated by this behavior, although she is in a compromised position as the male mounts. Females do occasionally refuse mounting or aggressively displace the male after mounting, even when Copulation Solicitation occurred just prior to the mounting attempt. It is also unclear why the male sometimes continues the Chitter vocalization throughout copulation.

Willoughby and Cade (1964) describe for the American Kestrel a Chitter vocalization that is similar to the Peregrine Chitter in terms of its contextual use, but which apparently signals "friendly approach." The apparent difference in meaning may be related to the very slight size dimorphism in Kestrels. Because of similar size, the male may be more intimidating as he prepares to mount, and a nonaggressive signal might ease the interaction. Kestrels also use a Chitter vocalization during Food-Transferring.

The copulation sequence in Peregrines is characterized by a series of "testing" actions and responses. When the sequence is initiated, by male or female, the female assumes the Copulation Solicitation posture, often facing away from the male. An alternating series then proceeds, with the female looking up toward the male, the male responding with the Hitched-Wing Display and components of the Agonistic Head-Low Bow, and the female then responding with renewed head-low postures. The series may be repeated several times. In a completed sequence the female will maintain the soliciting posture as the male flies to mount. Female termination of the sequence involves a shift from the nonaggressive soliciting posture to an anti-aggressive Display, the Extreme Head-Low Bow. Although this usually caused the male to abort his mounting attempt, in two experienced pairs the male frequently mounted anyway, and copulation was usually completed.

Observations on the incubating behavior of wild Peregrines, especially by Nelson (1970), permit an interesting comparison with captive pairs, suggesting a difference in the pair

relationship that may be important. In nature, the female controls the schedule of incubation duty. If the male is incubating as the female arrives on the nest-ledge, he gets up almost immediately and leaves (Nelson 1970, Wrege unpubl.). The reverse situation does not necessarily elicit female withdrawal. Exchanges for incubation proceed very differently in captive Peregrines. Although the female's dominance is usually evident, either sex may approach the incubating mate and try to urge the mate off the eggs. The success of such an attempt is variable. Interactions of this form indicate a fairly close adjustment of the pair to one another. Although a dominance relationship develops, successful breeding requires that it be stable enough for overt female aggression to be minimal, so that the male is not constantly intimidated by the female. In the wild, where male avoidance may be a frequent response to female pressuring, interactions can be more agonistic. Interactions for the most part are very short in wild pairs.

Gyrfalcons are slightly less dimorphic than Peregrines. Differences are not great in the relative frequencies of head-low postures. These postures are rare in the female and can be interpreted as a reduction in the use of head-low postures as approach-eliciting signals. As mentioned previously for Kestrels, the male Gyrfalcon is intimidating to the female, probably more so than in Peregrines. As a result, definitely antiaggressive postures are more usual in some ritualized displays, as are aggressive components in others. For example, Mutual Ledge Displays are characterized by constant head-low postures by both birds. In contrast to male Peregrines, the male Gyrfalcon also maintains the head-low posture while soliciting a Food-Transfer. We interpret this posture as approach-eliciting for two reasons: the male rarely takes food to the female, at least early in the season; and the female approaches in a partly aggressive, horizontal posture, indicating a fear component. Male Peregrines have very rarely been observed in approach-eliciting postures.

Aggressive components are obvious in the female Gyrfalcon's primary Copulation Solicitation. When the male is at some distance, the female may initially solicit copulation with a horizontal head-low posture and a nonaggressive Whine. As the male shows intention movements to mount, the female assumes an entirely horizontal posture oriented toward the male and gives a vocalization with many similarities to the Chitter used in aggressive contexts (figs. 3c and 3e). Our male was intimidated by this Display, alternating between the Curve-Neck Display and anti-aggressive Head-Low Bow. Mounting proceeded only when the female was not oriented toward the male. These behavior patterns are consistent with a situation involving an intimidating male and preceding an action during which the female is in a compromised position. As with Peregrines, the male precopulatory postures involve aggressive components. Although the Curve-Neck Display stresses a lowered beak, the body posture is vertical and tall, accompanied by a vocalization apparently identical to the Chitter of aggressive situations. It is not clear why Gyrfalcons and Kestrels differ in the aggressiveness of male precopulatory behavior. The difference may well be related to the aggressive components in female Gyrfalcon solicitation.

Unfortunately, observations of Prairie Falcons are limited; comparison with Peregrines and Gyrfalcons is more difficult. In our captive pairs the pair-bond appeared strained, and it is well known among falconers that Prairie Falcons are the most aggressive of the North American species of *Falco*.

There is no question of the dominant position of the female in our captives. Frequent displacement of the male by the female is characteristic throughout the breeding season. During the nonbreeding season the mates avoid one another.

The extremely pugnacious temperament of Prairie Falcons is not easily explained in terms of the degree of size dimorphism, which is close to that of Gyrfalcons. However, a com-

parison of the relative frequencies of some behaviors is instructive in relation to the decided female dominance. It is possible that the pairs observed in this study were less well integrated than sometimes occurs. Fyfe (1972) observed a captive pair that was "at ease" with one another.

During Male Ledge Displays, even more than in the other species, the male Prairie Falcon is aware of the female's location in the room. Immediately upon her approach for a Mutual Ledge Display, an extreme head-low posture is adopted. During the Display the male constantly bows or presses himself almost flat on the ledge.

Female Solicitation for Copulation in Prairie Falcons involves an extreme head-low posture almost always oriented away from the male. Often solicitation is silent. Hitched-Wing approach by the male is usual, but aggressive postures just before mounting are not conspicuous.

Relative frequencies of aggressive, anti-aggressive, and approach-eliciting behavior exhibited by male and female falcons support an interpretation of female dominance. The degree to which this dominance can be initiated and maintained by "passive" intimidation as compared to more overt behavioral actions appears to depend on the difference in size between the mates. Intimidation of the mate owing to size difference is probably the major factor controlling relative frequencies of agonistic behavior. The ratio of these frequencies in a given pair depends on their specific degree of dimorphism and on their history, while the agonistic components of ritualized display behavior may be related to the size dimorphism characteristic of the species as a whole. Preliminary analysis of quantitative data tends to support these qualitative interpretations (Wrege unpubl.).

4. *The Function of Vocalizations in Social Communication.* Preliminary analysis of the vocalizations in these four species indicates that variability in the contextual use of vocalizations can be considerable. Intergradation from one vocalization to another is particularly striking in Gyrfalcons and Lanner Falcons. Many courtship vocalizations used by captive Gyrfalcons are based on a single sound unit, differing only in the speed with which the units are repeated (figs. 3a and 3c). The vocalizations of Lanner Falcons have not been analyzed; however, they sound very similar to Gyrfalcons. In Peregrines and Prairie Falcons the structures of some vocalizations are more complex. Variability of the vocalizations in these species is in the degree of completeness of the basic unit and is associated with the motivational level or intensity of the behavior, not with specific contexts.

Figure 2a shows the most common vocalization in Peregrine courtship. In its complete form the Eechip has three parts, but frequently one or more parts are deleted or repeated. The contexts in which this vocalization is elicited range from low intensity Individual Ledge Displays through agonistic encounters. With the exception of the territorial Cack vocalization and the female Copulation Wail, all vocalizations are used in numerous contexts.

Apparently the primary function of vocalizations is to communicate the intensity of motivation. As intensity increases, either the speed of unit repetition increases (Gyrfalcons and Lanners, especially), or the sound unit is fragmented, with some parts repeated before a new unit is initiated (Peregrines and Prairie Falcons).

Summary

The courtship behavior of Peregrine Falcons, Gyrfalcons, Prairie Falcons, and Lanner Falcons was studied for the purpose of describing their reproductive behavior, and, using comparative analysis, to characterize the pair relationship. Twenty pairs of falcons were studied for two to four years with an emphasis on Peregrine Falcons.

We found the behavioral repertoire very similar in the species studied, with at least 75 percent of the postures and displays common to all. Most interspecific differences were in the frequencies of certain Display postures, and in the specific characteristics of vocalization. The function of these behavior patterns in pair integration is apparently the same for all species, making these similarities important management tools for the captive breeding of falcons. Experimental work on species most available or amenable to manipulation can be used to predict, with some confidence, the outcome of similar manipulations on captive Peregrines or other endangered species.

The vocalizations of these species are also similar in their basic structure and function. All the vocalizations show high levels of frequency modulation, causing the "noisy" appearance of the audio spectrographs (figs. 2, 3, and 4). This basic structure may be related to the open habitats utilized by these species (Morton 1975). A more important similarity is the intergradation of some vocalizations and their nonspecific contextual use. In captivity, each species uses many vocalizations to communicate the intensity of motivation, and very few to communicate the motivation to perform a specific action. Copulation Solicitation and territorial defense calls fall into the latter group.

The seasonal ontogeny of reproductive behavior in Peregrines follows a predictable pattern, at least in experienced pairs. In pairs remaining together all year, courtship is initiated earlier each year for about three years. Copulation begins several weeks before egg-laying and probably helps to strengthen the pair-bond. The third and fourth eggs in a clutch can be fertilized by copulations just before and after the second egg is laid. This suggests that artificial insemination can be achieved with minimal disturbance to the pair, providing the technique ensures the placement of semen directly into the oviduct.

The frequency with which displays and postures are expressed is the major interspecific difference in the behavior of the captive falcons studied. Such a difference is consistent with the hypothesis that female dominance is a characteristic of the pair relationship in large falcons and is possibly necessary for successful reproduction. Apparently the primary factor that influences the relative frequency of aggressive and nonaggressive behavior is the degree of size dimorphism between the sexes.

The pugnacious nature of falcons and the potentially very serious injury from aggressive encounters may be the causes of a behavioral repertoire with the capacity to transmit finely tuned information about motivation and its intensity. The amount of information communicated through postures is probably very high. Frequently birds change their response to their mate when little or no change in posture was observed. The vocalizations in each species seem well suited to signaling the intensity of motivation.

Acknowledgements

We would like to thank James D. Weaver, Kathy Johnson, and Bill Heck for their assistance with the collection of data, and Mike Hopiak for help in the preparation of figures. This study was supported in part by grant number GB 31547 from the National Science Foundation and by contributions to The Peregrine Fund. Support was also received from the National Rifle Association, National Wildlife Federation, Wildlife Management Institute, and the American Petroleum Institute.

Literature Cited

Amadon, D. 1975. Why are female birds of prey larger than males? *Raptor Res.* 9:1-11.

Brown, J. L. 1975. *The evolution of behavior*. New York: Norton.

Cade, T. J. 1955. Experiments on winter territoriality of the American Kestrel, *Falco sparverius*. *Wilson Bull*. 67:5-17.

———. 1960. Ecology of the Peregrine and Gyrfalcon populations in Alaska. *Univ. Calif. Publ. Zool.* 63:151-290.

Fischer, W. 1968. *Der Wanderfalk* (*Falco peregrinus und Falco pelegrinoides*). Die Neue Brehm-Bücherei, Berliner Tierpark-Buch Nr 13, Ziemsen, Wittenberg Lutherstadt (German Democratic Republic).

Fyfe, R. 1972. Breeding behavior of captive and wild Prairie and Peregrine Falcons. *Raptor Res.* 6 (Suppl. C):43-52.

Hagen, Y. 1942. Totalgewichts–Studien bei norwegisten Vogelarten. *Archiv. Natur.* 11:1-173.

Morris, J., and R. Stevens. 1971. Successful crossbreeding of a Peregrine tiercel and a Saker Falcon. *Captive Breeding of Diurnal Birds of Prey* 1:5-7.

Morton, E. S. 1975. Ecological sources of selection on avian sounds. *Amer. Natur.* 109:17-33.

Mueller, H. C. 1970. Courtship and copulation by a hand-reared Broad-winged Hawk. *Auk* 87:580.

———. 1971. Displays and vocalizations of the Sparrow Hawk. *Wilson Bull.* 83:249-254.

Nelson, R. W. 1970. Some aspects of the breeding behaviour of Peregrine Falcons on Langara Island, B.C. M.S. Thesis. University of Calgary, Calgary, Alberta, Canada.

———, and J. A. Campbell. 1973. Breeding and behavior of Arctic Peregrines in captivity. *Hawk Chalk* 11:39-54.

———, and J. A. Campbell. 1974. 1974 breeding and behavior of captive Arctic Peregrines. *Hawk Chalk* 13:44-61.

Platt, J. B. 1976. Gyrfalcon nest site selection and winter activity in the western Canadian arctic. *Can. Field Nat.* 90:338-345.

Weaver, J. D., and T. J. Cade. 1974. Special report on the falcon breeding program at Cornell University. *Hawk Chalk* 13:31-43.

Willoughby, E. J., and T. J. Cade. 1964. Breeding behavior of the American Kestrel (Sparrow Hawk). *Living Bird* 3:75-96.

THE PROPAGATION OF LARGE FALCONS IN CAPTIVITY

by
Tom J. Cade,
James D. Weaver,
Joseph B. Platt,[1]
and William A. Burnham[2]
Laboratory of Ornithology
Cornell University
Ithaca, New York 14850

Abstract

Wild falcons have been trained and held in captivity for more th three thousand years, but only in the last decade have falconers and other devotees made sustained attempts to propagate these birds. Since 1965, a worldwide interest has developed in perfecting methods for breeding birds of prey in captivity, particularly the large falcons.

The first consistent and encouraging results were achieved with American and European Kestrels (*Falco sparverius* and *F. tinnunculus*), although a German falconer, Waller (1962), had succeeded in breeding a pair of Peregrine Falcons (*Falco peregrinus*) in 1942 and 1943. Greatest interest has focused on the Peregrine because of the severely threatened state of breeding populations in North America and Europe and because of its high desirability as a bird for falconry.

Results in the last few years show that practical, large-scale production is feasible for most species, including the Peregrine. Some of the attempts to breed falcons are detailed in the references listed in table 1. At least fifteen species of *Falco* and three interspecific crosses have produced fertile eggs and reared young in captivity. The American Kestrel is an easy species to propagate, as is the European Kestrel; reproduction by first- and second-generation progeny has been obtained with both species. Among the large falcons, breeding by F_1 individuals has occurred with the Prairie Falcon (*Falco mexicanus*), Lanner (*Falco biarmicus*), and Peregrine Falcon. The Gyrfalcon (*Falco rusticolus*) was the most recent of the large species to reproduce in captivity, and it now seems likely that all species of falcons can be domestically propagated under the right circumstances.

The Peregrine Fund's research program was started in 1970 to develop techniques necessary for breeding falcons in captivity and to build up a captive population to produce a supply of birds large enough to reestablish breeding Peregrines in the eastern United States. Subsequently we extended our goals to include work with the severely endangered western *anatum* Peregrines, and we have also continued to work experimentally with other species, particularly the Prairie Falcon and the Gyrfalcon.

1. Present address:
Box 442
Awali, Bahrain
2. Present address:
1424 N.E. Frontage Road
Fort Collins, Colorado 80521

Table 1. Records of falcons reproducing in captivity.

Species	No. Breeding Females	Sources
AMERICAN KESTREL *Falco sparverius*	200+	Willoughby & Cade 1964, Koehler 1969, Porter & Wiemeyer 1970, Lincer 1975, Bird et al. 1976, G. L. Richards 1974, unpubl.
EUROPEAN KESTREL *Falco tinnunculus*	20+	Koehler 1969, Glasier 1972, Santer 1972.
LESSER KESTREL *Falco naumanni*	1?	Mendelssohn & Marder 1970.
*MAURITIUS KESTREL *Falco punctatus*	1	Temple 1975.
RED-FOOTED FALCON *Falco vespertinus*	1?	Fodor post-1964 (trans. 1971).
*NEW ZEALAND FALCON *Falco novaeseelandiae*	1	N. Fox 1976, unpubl.
RED-HEADED FALCON *Falco chicquera*	1	Koehler 1970.
ELEONORA'S FALCON *Falco eleonorae*	1	P. L. Whitehead 1975, unpubl.
MERLIN *Falco columbarius*	6+	Glasier 1972, Fyfe 1976, Campbell & Nelson 1975, L. H. Hurrell 1976, unpubl.
PEREGRINE *Falco peregrinus*	75+	Waller 1962, Beebe 1967, Schramm *vide* Peterson 1968, Meng 1972, Cade 1973, Fyfe 1976, Cade and Temple 1977.
LUGGAR *Falco jugger*	3	Dallimore 1972, Byron 1972, L. H. Hurrell 1974, unpubl.
LANNER *Falco biarmicus*	8+	Snelling 1973, Glasier 1972, Terrasse 1972, Trommer 1973.
SAKER *Falco cherrug*	2	Fodor post-1964 (trans. 1971), E. Laage 1972, 1973, unpubl.

GYRFALCON *Falco rusticolus*	7+	Cade 1974, 1975; Cade & Dague 1976, Fyfe 1976, E. Müller 1976, unpubl., L. G. Swartz 1976, unpubl.
PRAIRIE FALCON *Falco mexicanus*	30+	Kendall 1968, Enderson 1971, Fyfe 1972, Cade 1972, 1973, 1974; Burnham & Heinrich 1976.
INTER-SPECIES CROSSES *F. peregrinus* male X *F. cherrug* female	1	Morris & Stevens 1971, 1972.
F. peregrinus male X *F. rusticolus* female	2	Cade and Weaver 1976.
F. mexicanus male X *F. peregrinus* female	1	Boyd and Boyd 1975.

*Chicks died accidentally before flying.

Table 2. Birds of prey produced through domestic breeding by the Peregrine Fund at all facilities, 1972-1976.

Falco peregrinus	Peregrine Falcon	137
Falco biarmicus	Lanner Falcon	27
Falco mexicanus	Prairie Falcon	68
Falco rusticolus	Gyrfalcon	14
Falco sparverius	American Kestrel	25
Falco rusticolus X *F. peregrinus*		4
Parabuteo unicinctus	Harris Hawk	5
Aquila chrysaetos	Golden Eagle	1
Buteo jamaicensis	Red-tailed Hawk	1
Accipiter gentilis	Goshawk	6
	Total	288

The main facility is located at Cornell University, but a similar-sized operation was established in 1974 at Fort Collins, Colorado, in collaboration with the Colorado Division of Wildlife. Cooperative private breeding lofts also exist in Pennsylvania under R. B. Berry's management and in New Mexico under F. M. Bond. In its brief existence the Peregrine Fund has produced 288 fledged birds of prey through domestic propagation (table 2).

The purpose of this paper is to present a detailed description of the procedures used and the results of their successful and unsuccessful applications. The data relate

primarily to Peregrines and secondarily to other large falcons. This report also serves to update and correct a previous one by Weaver and Cade (1974, BPIE no. 90).

Facilities and Maintenance

The Cornell facility is a pole barn 69 m long by 14 m wide, with steel roof and siding at the ends. It is divided into 36 chambers 3 by 6 m in area and 2 that are 6 by 6 m, plus various utility and office areas (fig. 1). Each chamber is 5.5 m high at the apex and 4.3 m at the eaves. The entire sidewall is open to the weather but enclosed on the outside by 13 mm welded wire mesh and on the inside by 13 mm tubular steel, vertical bars, spaced 63 mm apart. The lowest meter of this wall is covered with a sheet of fiberglass to prevent the drifting of snow into the chambers. The roof provides complete cover with a single 60-cm-by-240-cm sheet of white, translucent fiberglass in each room to allow for additional light from above.

In Fort Collins we have three separate buildings of 12 chambers each. The work and utility areas are separate from the birds. We feel that this arrangement minimizes the chance of total loss from fire or disease. The individual chambers are identical, with a few exceptions. Higher water pressure has made possible the use of a remote watering system that allows bath and drinking water to be changed by periodic flushing without anyone's entering the room. Owing to the drier climate we have also been able to do away with the fiberglass panel in the roof. The opening remains but is barred and screened, allowing more light and air to enter.

Floors are coarse gravel fill covered with at least 5 cm of pea-sized, washed gravel. All chambers are cleaned twice a year. Floors and lower walls are sprayed once a year with a 10 percent formalin solution by an attendant who wears a gas mask. Perches and nest ledge gravel are cleaned and renewed as needed. Birds are moved to holding rooms while the chambers are being cleaned. The chambers are allowed to dry and air out thoroughly before the birds are replaced. Each chamber has fixtures for water, as well as for artificial lights, operated by manual switches or automatic timers from the observation corridors. The layout of a typical chamber is shown in figure 2.

The rooms are furnished with a variety of ledge-type perches arranged at different heights on the walls and with a natural branch that extends 1 m from the wall. We try to keep the middle space of the room free for unobstructed flight and therefore do not place any beams or branches across the full width of the room. There are two nesting ledges in each room (fig. 2). Pairs usually have a preference for one ledge or the other for their first clutches year after year. When we take the first set of eggs for artificial incubation, the female often switches to the other ledge for her second set, as falcons usually do in nature. We recorded the deposition sites for 30 clutches laid by our three most productive pairs. Seventeen times a clutch was removed and a subsequent clutch laid; only 5 of the subsequent clutches were laid on the ledge from which a clutch had just been removed. In the sample of 30 clutches half were laid on ledge 1 and half on ledge 2.

We routinely feed through ports located above a shelf 1.5 m from the floor, but an alternate feeding port is located high on the back wall above shelf 6 (see fig. 2) for special use. The diet consists of five-week-old chickens and Coturnix Quail (*Coturnix coturnix*), the latter forming the bulk of the diet during the breeding season. No vitamin supplements are given. Quail and chickens are raised at the facility; chickens are maintained on unmedicated chick starter and quail on a higher protein game-bird

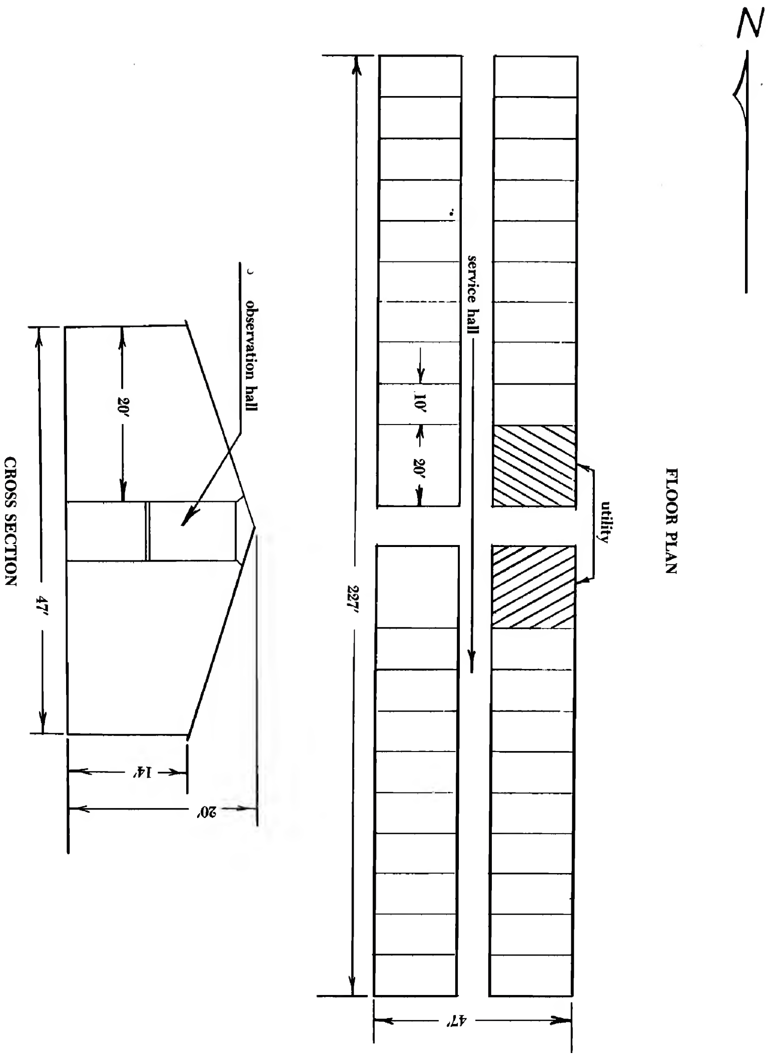


Figure 1. Floor plan and cross section of Cornell University facility.

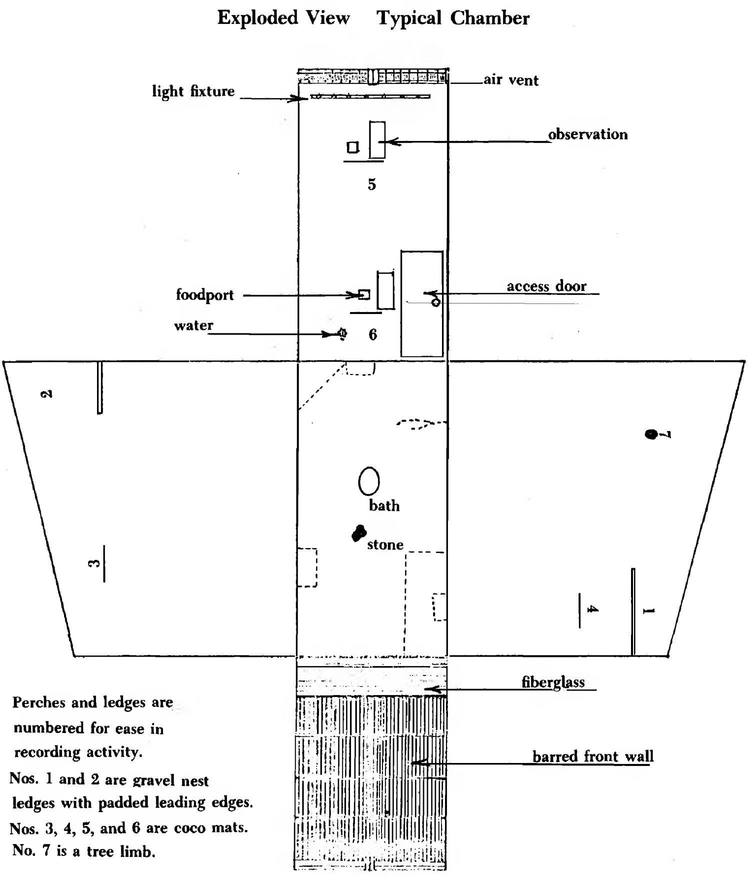


Figure 2. Exploded view of typical chamber.

starter. Carbon dioxide is used to kill these animals as they reach the desirable size. The quail and chickens are allowed to fast for 24 hours prior to killing, thereby eliminating the mess that results from the remains of engorged digestive tracts. No live prey is provided, and all food is given fresh or kept frozen until needed. To avoid confrontations over a single food item, pairs are given two or more pieces. During periods of courtship activity, smaller pieces are provided several times per day, sometimes through the upper foodports. This procedure serves to reinforce the pair bond by increasing the number of opportunities the male has to present food to his mate. Whole quail are particularly valuable for this purpose as they seem to be the preferred food and offer an opportunity for an almost ritualized plucking response by males prior to transfer to their females. Food objects for courtship-feeding should be small enough so that the male can easily pick them up in his beak and fly with them.

To avoid trouble with disease and insects, cached food items are not allowed to accumulate. A day with no feeding or a late feeding usually eliminates cached food. At Cornell someone enters the chambers regularly to exchange bath pans. Water is always available, except on the coldest days when it freezes. A large stone on the floor near the bath serves as a perch should a bird be too wet after bathing to regain one of the low wall perches. Perches and other furnishings are arranged in such a way as to keep birds off the floor as much as possible, since it is the area of greatest accumulation of droppings and food remains. Two concrete, block-sized stones are placed prominently on the nest ledges to provide wear on talons; these stones are often preferred perches.

All nest ledges can be observed through one-way glass. Being able to observe the falcons without disturbing them allows us to monitor their progress in the nesting cycle and to intervene if undesirable behavior develops.

The photoperiod for arctic Peregrines and Gyrfalcons is increased beginning February 1. The natural day length is increased by 30 minutes of incandescent light added at the beginning of the photoperiod every week until a total of 16 hours is reached about April 1. This photoperiod is maintained through the rest of the breeding cycle. In midsummer the breeders are returned to the natural photoperiod of the Ithaca region.

Selection of Breeding Stock

Peregrine Falcons removed from the wild before fledging are much more likely to breed in captivity than are falcons trapped after independence, although several cases have now been reported in which wild-caught postnestlings and adults have reproduced in confinement. The Peregrine Fund has held wild-caught Peregrines in breeding chambers for several years with no success, as have a number of other projects.

Falconer's birds removed from the nest and hand raised without other falcons may breed, but the risk of failure is great. Ideally, we feel birds intended for breeding stock should be fledged in small groups by adult falcons whether they are removed from wild eyries as downies or hatched in captivity. After fledging they should be housed in groups through their first molt. Such treatment prevents imprinting on humans and provides a more normal social development.

The most common cause of breeding failure in mature pairs is abnormal behavior by one or both birds. A bird can become sexually imprinted on humans because of close association with its keeper before fledging. Thus, it partially or completely fails to respond sexually to its mate when of breeding age. Imprinted females may lay

eggs, and imprinted males may produce sperm, but their sexual displays are addressed to people, and they often respond aggressively toward their conspecific chamber mates.

The ontogeny of breeding behavior is quite similar in pairs that are properly raised. Twelve-month-old Peregrines show only sporadic and incomplete courtship activity even when housed as pairs in breeding chambers. At the onset of their second spring, males begin scraping and attempt food transferring. Mutual activities such as food transferring and ledge displays are often incomplete because one or the other falcon responds improperly. It is interesting to note that two females laid eggs (infertile) when only 2 years old; both, however, were paired with 3-year-old males. Wrege and Cade (1977) described in detail the timing and expression of courtship behavior as it normally occurs in fully mature pairs in their third or fourth year.

Copulation usually ceases with the laying of the third egg, but food transferring continues. Females perform most of the incubation. When the eggs are removed after 7 days of incubation, the pair begins scraping almost immediately, but copulation does not occur for 7 to 10 days. The first egg is usually laid 14 days after the previous clutch has been removed, but in a few cases not until the 15th or 16th day.

Peregrines are indeterminate layers. Our females have laid 11 and 12 eggs when no more than 2 eggs were left in the nest. Of 33 undisturbed Peregrine clutches, 25 had 4 eggs, 3 had 5 eggs, and 3 had 3 eggs, for an average of 4.0 eggs per clutch.

Artificial Insemination

When normal mating does not occur in a pair, artificial insemination can often be used to achieve fertilization, particularly with birds that are in some degree sexually responsive to human beings and produce mature gametes. Fourteen female Peregrines and two Gyrfalcons have been artifically inseminated, and we have obtained semen with motile sperm from ten male Peregrines and two Gyrfalcons. All female falcons except one Gyrfalcon had to be forcibly inseminated.

We obtain semen by wrapping the hooded bird in a towel and placing him breast down on a pad of foam rubber, his feet being gently pulled back and down from his tail. One person holds his feet and a fire-polished 1-by-100-mm capillary tube. A second person strokes the bird along his back and sides from the rib cage to the cloaca. The middle fingers of the other hand stroke his abdomen from the keel to the cloaca just slightly ahead of the side and back stroke. After a few preliminary motions, a final stroke is made with increased pressure. The abdominal stroke is stopped at the pubic bones, but pressure is maintained while the side stroke continues to the cloaca where it terminates in a gentle squeeze causing any semen to be expelled. It appears as a drop of semiclear, viscous fluid and is collected by touching it with the end of the capillary tube. Additional stroking will produce more semen. We recommend that no more be taken than is needed if the male is to be used again in a day or so. The minimum safe volume for one insemination is $10\,\mu$ l. Microscopic examination of a sample from the last of a series of droplets will usually reveal an increased number of immature spermatazoa not capable of fertilizing the eggs. If a particular male is to be used daily, the sperm count, and not the quantity of semen, will be the main factor that determines his usefulness for artificial insemination. We generally try to obtain semen from a bird no more often than every other day, taking 30 to $50\,\mu$ l. Males have produced quite consistently over a 6-week period; however, we have also had males stop production after an initial handling. Other methods are also effective,

such as the one devised by Steve Baptiste of Reno, Nevada, in which the male is placed on his back. Bird et al. (1976) describe other methods used successfully on Kestrels.

We have used two techniques for insemination. Until 1976 females were simply held while the capillary tube was inserted a few mm into the cloaca and the semen forced out. Encouraged by the success of Boyd (1974) and Bird et al. (1976), we began everting the oviduct and placing the semen directly into it. This procedure entails some risk to the falcon and should be attempted only by those who have witnessed it and practiced it under the guidance of an experienced person.

To be safe, the female should have laid an egg no more than 12 hours before the attempt to evert the oviduct. Sooner after laying is better, as this timing insures she will not have an advanced egg that could be broken in the oviduct during handling. We generaly inseminate after each egg to fertilize the second egg to follow. The bird is hooded, wrapped in a towel, and placed on her breast. Her feet are pulled gently down and away from her body. To evert the oviduct, the thumb and two fingers of one hand partially roll back the lips of the cloaca while pressure is applied to the abdomen with the fingers of the other hand. This steady pressure is maintained throughout the insemination. It is this pressure on the viscera that causes the oviduct to protrude from the cloaca. It appears as a red-purple hemisphere with the opening being an off-center indentation to the bird's left side.

To inseminate, rubber tubing about 40 cm long is attached to the vacant end of the capillary tube containing the semen. The capillary tube is then carefully slipped into the entrance of the oviduct to a depth of no more than 15 mm. The oviduct walls are very delicate and can be punctured by rough treatment. After the glass tube is inserted, the semen is expelled by gently blowing (almost breathing) through the tubing. Blowing too hard causes the semen to flow back out of the oviduct and has the potential of damaging or infecting the oviduct.

As the tube is withdrawn, the pressure on the belly is released allowing the oviduct to return to its normal position. Inseminations are done in the chambers and require less than one minute. Eversion of the cloaca and oviduct increased our rate of successful artificial insemination from 27 percent to 73 percent (table 3). Again, other methods of insemination can be used—both forced and cooperative (Berry 1972, Temple 1972, Boyd 1974, Bird et al. 1976).

Artificial insemination is a common practice in the poultry industry, and a great deal can be gained from working with these people and becoming familiar with their literature. Valuable experience can be had from practicing with chickens, ducks, and even pigeons. The birds must be in breeding condition, and it should be remembered that an oviduct is easier tc evert if an egg has been laid recently.

Laying

The laying of eggs usually occurs about 2-4 weeks after the first copulation. The female enters a condition known as "egg-laying lethargy" (Olendorff 1968) about 5 days before the first egg. She spends more and more time in the scrape and appears to be ill. Her eyes are often half-closed; she dozes and appears to move with difficulty. Her cloaca and lower abdomen are swollen. When she excretes, she does so in a squatting, spread-legged posture. The excretion is voluminous, and the enlarged lips of her cloaca are conspicuous and rosy. This lethargic condition persists throughout egg-laying but in varying degrees. Eggs are generally laid at approximately 48-hour

Table 3. Relative success in fertilizing Peregrine Falcons by two methods of artificial insemination.

Semen Placement	Number of Females	Number of Eggs Laid	Number of Eggs Fertilized	Percent Fertilized
In oviduct	10	45	33	73
In cloaca	3*	22	6	27

*One female during two seasons and one female during one season.

intervals, but instances of a 72-hour interval are not unusual. Drops in ambient temperature may cause such delays.

Incubation

Full incubation begins with laying of the last egg, typically the fourth, but individual females may begin partial incubation with the second or third egg. Actual incubation differs from "standing over" or "laying on" the eggs. The erection of the feathers on the lower back and rump and vigorous settling and shuffling motions indicate that actual incubation is under way. With incubation both birds begin to exhibit total attentiveness to the eggs. At times prior to the completion of the clutch, activities at the scrape seem to endanger the existing eggs in that they may be kicked completely out of the scrape by overzealous scraping, usually by the male. The female will usually roll them back within a few hours.

We have had experience with 14 pairs of Peregrines, 1 pair of Lanners, 1 pair of Gyrfalcons, and 5 pairs of Prairie Falcons that exhibit normal brooding behavior. Such birds are allowed to incubate their eggs for 7 days after completion of the clutch. The eggs are then placed in an incubator. Seven days is an arbitrary compromise. Since we want the pairs to recycle, there is an advantage in removing the eggs as soon as possible, as the longer the pair incubates the less likely they are to recycle. On the other hand, it is important to give the eggs some natural incubation, since it is known that this experience increases the hatchability of wild birds' eggs that are artificially incubated. The eggs are placed in modified Marsh Farms Roll-X forced-air incubators. They are placed large end up in a chicken egg-sized grid and turned by hand at least eight times a day. Temperature is monitored with high quality mercury thermometers. Because temperature varies within the unit, the thermometer is placed very near the eggs. Humidity is monitored with a wet-bulb thermometer or hair hygrometer and modified by varying the amount of water present in the incubator. The eggs are weighed and candled every 5 days. The breeding results for all our falcons for the years 1973-76 are summarized in table 4.

Our program has produced 216 fertile Peregrine eggs in 4 years. Seventy-two percent (156) of them hatched. A four-egg clutch of *F.p. tundrius* eggs requires 32 days from the laying of the last egg to the hatching of the last chick. Thirty-five days are required for a clutch of *F.p. pealei* eggs to hatch. Usually three chicks hatch simultaneously and the fourth a day later. It is important to note that the number of days required for an egg to hatch in an incubator is a function of temperature and humidity. An experiment conducted by Card and Nesheim (1973) involved three machines operating at the same dry bulb temperature (99° F) but with different humidities. Wet bulb temperatures in the machines were 75°, 85°, and 90° F, respectively. These correspond to 35, 56, and 70 percent relative humidity. A spread of 48 hours

existed in hatching time between the first and third machines. When the temperature in the low-humidity machine was adjusted to 100° F, and that in the high-humidity machine adjusted to 98° F, all three machines hatched chicks in the normal 21-day period for chickens. The number of days required to hatch can be critical, as the degree of yolk-sac absorption may be affected, and unretracted yolk-sacs may occur at hatching; however, many other factors can also cause unretracted yolk-sacs.

Table 5 presents the conditions we consider optimum for artificial incubation of eggs after 6-7 days of natural incubation. Under these conditions 85 percent of the eggs (52 of 61) incubated hatched; however, individual eggs respond differently. The crucial determinant of the embryo's environment for successful hatching is the amount of water loss. Depending on their size, Peregrine eggs must lose 0.7 to 0.9 grams per 5 days of artificial incubation. The relative humidity can be modified within limits to increase or decrease weight loss after each weighing, when it has been determined that an egg is losing too much or too little moisture.

We calculated weight loss from laying to hatch for 63 eggs of various species and subspecies of large falcons (table 6). The average of 16 percent approximates the 18 percent predicted by Rahn and Ar (1974). Though data are limited, severe decreases in hatchability occur when weight losses are lower than 14 percent and higher than 20 percent. When figuring weight loss per day, the 2-day loss from pip to hatch must be considered separately since it will be more than twice the prepip losses. The figures (table 6) are presented only as a guide and may not prove optimal for all eggs under all conditions; but all these eggs produced viable chicks.

Table 4. Summary of breeding performance by falcons in the Peregrine Fund projects.

	No. Laying Females				No. Fertile Females				Total Eggs Laid				No. Eggs Fertile				No. Eggs Hatched				No. Young Raised			
Species	'73	'74	'75	'76	'73	'74	'75	'76	'73	'74	'75	'76	'73	'74	'75	'76	'73	'74	'75	'76	'73	'74	'75	'76
Peregrine	4	6	11	25*	3	5	8	21	41	59	109	191	26	34	44	112	22	24	27	83	20	23	25	69
Gyrfalcon	1	2	2	3	0	1	1	3	7	14	14	24	0	6	8	13+	0	3	6	13	0	2	3	13
Lanner Falcon	2	1	1	1	2	1	1	1	12	11	8	10	9	10	8	10	6	8	6	8	6	7	6	8
Prairie Falcon	5	5	7	1	2	5	7	1	27	38	47	5	14	35	38	5	7	30	34	3	7	29	30	2

*Includes one successful pair at Bob Berry's facility.
+Includes four hybridized eggs.

Table 5. Most successful conditions for artificial incubation of eggs after six to seven days of natural incubation.

Species	Temperature Degrees Fahrenheit	% Relative Humidity[1]
Falco peregrinus tundrius	98.5–99.2	40–45
Falco peregrinus pealei	98.5–99.2	45–50
Falco peregrinus anatum		
(New York)	98.5–99.2	35–40[2]
(Colorado)	98.2–98.9	25–30
Falco peregrinus brookei	98.5–99.2	35–40[2]
Falco mexicanus		
(New York)	98.5–99.2	35–40
(Colorado)	98.2–98.9	25–30
Falco rusticolus	98.5–99.2	15

[1]Relative humidities must be manipulated to insure proper water loss from the egg.
[2]These humidities have not been properly tested; there is evidence that they are too high.

Table 6. Weight loss percentages for falcon eggs.[1]

Species Subspecies	Percent of Fresh Weight[2]	Number of eggs
Falco peregrinus pealei	15	4
Falco peregrinus tundrius	16	4
Falco peregrinus brookei	16	3
Falco peregrinus anatum	16	2
Falco mexicanus	18	42[3]
Falco biarmicus	15	4
Falco rusticolus	16	4

[1]Selected representative figures for successfully hatched clutches.
[2]Loss from day 1 to hatching.
[3]Burnham and Heinrich (1976).

The relative humidities listed in table 5 produce the desired weight loss for successful hatching. It is interesting that the *pealei* subspecies requires a higher humidity than other North American Peregrines. It is a race native to the humid coasts of British Columbia and Alaska. We examined Peregrine eggshells using a scanning electron microscope (A. Schwartz et al., unpublished manuscript). The shells of *F.p. pealei* have larger pores than those of *F.p. anatum*. Wild Gyrfalcons, on the other hand, incubate at low relative humidities because the ambient temperatures are between +5° and -40° C (Platt 1976). It will be most interesting to see how the shells of Gyrfalcons and Prairie Falcons compare with those of Peregrines.

At Cornell University three fertile *F.p. anatum* eggs were incubated full term by their parents. Only one egg hatched, and the chick from it was abnormal. The two dead full-term embryos were edematous; perhaps the high (above 50 percent) relative humidity of the Ithaca region was too great. The adults are from New Mexico.

Artificial Incubation of Eggs from Day 1

Pairs not exhibiting normal nest attentiveness and females whose clutches we wish to extend have their eggs removed as they are laid. Artificial incubation at 98.5 to 99.2° F from the day of laying has proved to be less successful than if some natural incubation has taken place. We have tried several techniques to improve our success.

Two fertile eggs were removed from a highly successful pair on the day they were laid and placed in a 90° F incubator. The temperature was increased 1° F per day until 98.8° was reached. The embryos ceased development early in their incubation.

Foster parents successfully provided the start with natural incubation needed to hatch eggs removed from their parents at day 1. Either all fertile eggs placed under a setting Lanner or Prairie Falcon hatched in our incubators, or their failure was attributable to some factor other than their early incubation under a bird.

In 1976 we removed 46 eggs from females that had been artificially inseminated and were unwilling to incubate. To start such a large number of eggs we used Silkie Chickens. Falcons' eggs were stored at 5° C until a clutch could be formed or were placed under a hen a few hours after being laid. Of the fertile eggs started by Silkies, 84 percent hatched (7 out of 10 Peregrine, 6 out of 6 Gyrfalcon, 4 out of 5 Lanner, and 3 out of 3 hybrid eggs).

For chickens, whether they are Silkies, Cochens, or another breed, to provide the greatest benefit, they must be conditioned properly to the point of being completely

tame so that they may be handled easily. To accomplish this end they are handled and fed special handouts each day at a particular time. They will come to look forward to this routine, and this reward is important if they are to be trusted with special duties. They may then be picked up from nests without struggling and possibly breaking eggs.

Broodiness can be brought on by an increase in photoperiod, provision of nesting sites and materials, and the presence of a rooster. Once a hen becomes broody over her own eggs, she is placed on a similar nest of crushed sugar cane litter, which contains the falcon eggs. When hens are incubating, other birds should be excluded. We lock the hen in a nest box with her clutch of eggs. Each day at the appointed time we remove the hen to let her eat, drink, and defecate. We place her back on the eggs about 20 minutes later.

In 1973 and 1974 all incubating eggs were cooled to room temperature twice daily for 10 minutes. No benefit (or harm) could be attributed to the practice, so it was stopped as production increased.

Hatching

About 48 hours before the chick first pips the shell, the air cell within the egg begins to expand and may extend halfway down one side of the egg. This change is necessary to provide the chick with room to turn inside the shell; it also indicates that proper water loss has occurred during incubation. Chicks that have not lost sufficient moisture prior to this time are edematous; their larger size and lack of muscle tone prevents a successful hatch even though they may be able to pip the shell. When an egg has pipped (developed a small bump and tiny crack in the shell), it is placed in a still-air hatcher with a slightly lower temperature (98° to 98.5° F) and a much higher relative humidity, up to 80 percent. The eggs are placed on their sides with the pips uppermost. Normally the chicks are left alone to complete the hatching process. If water loss has been adequate prior to pip, and if the membranes are not allowed to dry out after pipping, hatching occurs about 55 hours after pipping (range 24 to 78 hours).

We monitor the chick's condition by noting its movements at the opening in the shell and by listening to its vocalizations. Assisting the chick out of the egg is done only as a last resort. The membranes surrounding the chick contain blood vessels which must be shut down before hatching. Premature rupture of these vessels by "helping" is fatal. The eggs may be misted with water to retard desiccation of the membranes during the last half of hatching. Dry membranes become leathery and retard hatching. The drying of membranes generally results from opening the hatcher too often to check progress.

The approximately fifty hours necessary for a successful hatch are spent largely in periods of inactivity. After pipping, the chick "breaks up" an area 10 to 20 mm in diameter around the pip. The chick, turning within, begins to cut the egg open by scoring the shell. The time required to complete the turn varies from 20 minutes to several hours.

An unretracted yolk-sac is the most frequent problem we have encountered with hatching chicks. It is possible to reduce partially unretracted yolk-sacs, up to 20 mm in diameter, by gently forcing the yolk into the body cavity with lubricated fingers. If this fails, the protruding sac must be ligated and removed. Using surgical gut, one can ligate the sac at the sphincter and cut it off 2 mm below the knot. The chick

will need special feeding, smaller amounts more frequently, as well as a vitamin and mineral supplement to substitute for the loss of the yolk, necessary for early growth and bone development. The prognosis is generally good, but the real task is to discover which of the various incubation conditions was responsible for the problem.

Three chicks were malformed at hatching. Two sibling Prairie Falcons had abnormal muscle control. Even when 14 days old they were not able to lift their heads or sit up. Bone and feather development appeared normal, and their brood mates were normal. A possible cause was that they were produced by a brother-sister pair, which itself was produced by a brother-sister pair. A single Peregrine was hatched with slightly malformed feet and beak. He was the only chick to hatch from three fertile eggs incubated by their parents during a period of very high ambient humidity. Although he developed normally, he was abnormally active. His nest mates killed him at 20 days of age.

Of the 156 Peregrines hatched, five died exhibiting symptoms of rickets. It should be noted that four of these five hatched with unretracted yolk sacs. The removal of the yolk sac may have reduced the calcium phosphate available to the chick or the vitamins required for calcium mobilization into bone.

Posthatching

Hatched chicks receive an antibiotic salve on the umbilicus and are placed back in the hatcher for up to 1 day. Two to four chicks of the same age are then placed in a 40-mm-deep disposable aluminum pan containing 30 mm of San-i-cel, a sanitary litter made from ground corn cobs. Wood shavings or sawdust can be more easily eaten by eyasses and should not be used as nest material. The pans are placed in brooders. Temperature is regulated by an ether wafer thermostat and heat coil. For the first few days the temperature is kept at 95° F, but afterward it is reduced 1° F per day until the chicks begin to thermoregulate at room temperature. The behavior of the chicks provides clues to help determine the correct temperature. They huddle, shivering and cheeping, when cold and lie apart from one another with wings and legs outstretched when too warm. They are comfortable when they quietly sleep while touching one another.

The first food is provided 12 to 18 hours after hatching. A gaping response can be elicited by the handler's giving an imitation of the "chup" call of the adult as he presents a tiny shred of meat on blunted forceps. The young are fed freshly killed and ground whole Coturnix Quail with the skin, digestive tracts, and feet removed. Quail are killed without loss of blood, which acts as a moisturizer for the ground mass. The task of feeding a number of older young is made easy through the use of disposable plastic bags. A bag is filled with ground food, the corner is snipped off, and then it is used much like a cake decorator, by squeezing out bite-size portions into the chick's gape. Each bird can be given its allotment in a few seconds. Ground 5-week-old chickens are gradually worked into the diet as the young reach 10 days of age. No casting or vitamin supplement has been given in the past, but we will begin using Vionate (Squibb) in small amounts during our 1977 season. The chicks are fed small meals every 2 to 4 hours for the first few days. As soon as food can be seen building up in the crop, the meal is over. Excess food may spoil in the digestive tract and result in poisoning, a very real possibility. As the young grow, crop capacity increases; hence, meals become larger and less frequent. Feedings are given only on empty crops.

Return of Young to Parents

Young are introduced to adult Peregrines when they are 15 to 20 days old. We return young only to adults that are sitting on eggs or feeding young. If adults have never fed young, we test their reaction with a Lanner or Prairie Falcon chick. The chicks have no problems relating to adults. Some adults will not accept young and may attempt to kill or remove them from the scrape. The sudden arrival of the adults on the nest ledges causes the older young to hiss and exhibit a defensive attitude, but this condition rarely extends into the second day. Reaction of the young to the "chup" call of the female adult is immediate. Pairs that will care for one or two young can be given as many as six at a time with no problem. One female Prairie Falcon successfully fed and fledged eight young. Pairs have been given new broods of downy young as older broods are removed.

No aggression between adults and their fledged young has been seen even when the young are left with adults for several months. Usually, however, young are placed in large rooms (double chambers) containing Peregrines of similar ages a few weeks after fledging. Some birds are left in these large chambers until after their first molt. Such groups of falcons must be watched, especially after one year of age, to make sure aggression does not become too severe.

Discussion and Conclusion

Much progress has been made in the *domestic breeding* of falcons since 1970 (see Jack 1977 for terminology). Whereas at that time only kestrels had been produced in large numbers, now impressive numbers of Peregrines, Prairie Falcons, Lanners, and Gyrfalcons are being raised each year, and it is only a matter of time before the Saker and some other species are included among those that reproduce regularly under domestic husbandry. As we noted earlier, it is likely, in fact, that all species of the genus *Falco* can be induced to breed in captivity, once the right set of conditions has been determined for each case.

The major technical hurdles have been surmounted, at least sufficiently so that utilizable numbers of some species—Peregrine, Prairie Falcon, Gyrfalcon, and Lanner—have become available. Reproduction by members of F_1 and F_2 generations has occurred for several years among domestically propagated kestrels and, recently, reproduction by F_1 individuals among Peregrines, Prairie Falcons, and Lanners. It appears probable that self-sustaining domestic populations are realizable, barring unforeseen problems in reproduction by subsequent generations of progeny.

This prediction means that endangered forms (gene pools) can be perpetuated indefinitely by domestic breeding and husbandry. Rare species such as the Mauritius Kestrel (*Falco punctatus*), Teita Falcon (*Falco fasciinucha*), Orange-breasted Falcon (*Falco deiroleucus*), and Kleinschmidt's Falcon (*Falco kreyenborgi*) immediately come to mind. With the proven techniques we now have for propagating birds of prey in captivity, there is no reason why any species has to become extinct, although some may eventually no longer be able to survive as wild populations. There is no reason why any species should become so rare that reasonable use of individuals for falconry, scientific study, or other legitimate purposes cannot be justified.

At the Conference on Raptor Conservation Techniques, convened by the Raptor Research Foundation in 1973, Cade (1974) outlined three basic reasons why a number of people have become involved in attempts to breed Peregrines and other raptors in

captivity. The first concerns our human nature to respond to challenging circumstances and to try to succeed in an undertaking that most people consider impossible to accomplish. Thus, from the standpoint of personal motivation, the breeding project "becomes an exciting intellectual and technological game—a true form of recreation and competitive sport—in which science and craft become inextricably bound together."

Today, stretching across the North American continent and, indeed, over much of the world, there is a network of private and institutional breeding projects that will insure continuing progress in the domestic propagation of raptors and the husbandry of sufficient numbers of birds so that all interests in the Peregrine and in other falcons can be satisfied. Thanks in no small degree to the early leadership and focus of the Raptor Research Foundation, there has been, and continues to be, close communication and cooperation among the private breeders and institutional programs. We believe that this is the main reason why the breeding of falcons in captivity has made such rapid progress.

Kenward (1977) has recently tabulated world figures to show that, as of 1975, the private breeders—mostly falconers—have raised half of all the Falconiformes produced in captivity. We cannot emphasize too much the importance of dedicated and qualified private breeders as continuing sources of new information and techniques and as husbanders of the reserve breeding stock from which future generations of birds will come. The Peregrine Fund currently enjoys close working relations with eight private breeding projects in the United States and with one overseas, as well as with the CWS program in Canada, and we have always tried to make our information fully and freely available to all.

With the level of friendly competition and enthusiasm running high among breeders, the remaining problems in domestic propagation of the large falcons should be quickly resolved. The principal ones still are (1) incompatibility between some mates and their failure to copulate, even though full gonadal development may occur, and (2) artificial incubation and hatching of eggs. If all eggs laid by falcons in our program had been fertile in 1976, and if 80 percent of them had hatched (a reasonable expectation), we would have produced 184 chicks instead of 107. There are still plenty of challenges to test a breeder's ingenuity and knowledge.

A second reason why the domestic breeding of birds of prey has become popular and successful is that most of the people involved are falconers, who have a single-minded, even fanatical, devotion to raptors and 3,000 years of evolved technology at their command for handling and caring for them in confinement (Nye 1976). Many North American and European falconers had realized by 1970 that the future of their sport would depend upon developing methods for captive propagation and the eventual use of domestic birds for hunting—particularly in the case of the Peregrine and the other large falcons, for which so much concern has been expressed by conservationists. All the early successes in breeding large falcons in captivity were accomplished by falconers (see table 1), and institutional programs have relied heavily on the techniques of falconry and on personnel trained as falconers to produce the large numbers of Peregrines required for restocking programs.

Now falconers are beginning to enjoy the fruits of their early vision and labors, as a fair number of domestically propagated hawks and falcons are being flown in the field. In North America these birds include several Prairie Falcons, Gyrfalcons, Lanners, Peale's Peregrines, Goshawks, Harris' Hawks, and one Golden Eagle; in Europe,

several Peregrines, Gyrfalcons, Lanners, and Merlins. Initial reports (Adamson 1974, Shor 1975, Cade in press, L. Hurrell pers. comm.) indicate that these domestically bred hunters acquit themselves at least as well as wild-taken eyasses, and we agree with Smylie and Bond (1975) that a new era in falconry has emerged as a result of domestic breeding. American and European falconers have already embraced domestic breeding as their salvation insofar as continued use of large falcons is concerned. We believe this view will have to be accepted by falconers worldwide before long. In fact, it is already a matter of considerable pride with some falconers that they do not take falcons from the wild any more in order to practice their sport.

The third reason for domestic breeding is to produce a supply of Peregrine Falcons that can be used to restock natural areas where the species has disappeared or been greatly reduced as a breeding bird. Our level of production in the Peregrine Fund's projects has been high enough to allow us to begin some experimental releases of domestically produced Peregrines in 1974, 1975, and 1976, both in the East and in the West. We have now released a total of 62 young Peregrines into nature, 7 by fostering to wild parent Peregrines in Colorado and 55 by hacking at 10 sites in seven eastern states. The Canadian Wildlife Service's project under Richard Fyfe (1976) has put out a similar number, so that the total North American effort will soon assume the proportions of an operational program.

Cade and Temple (1977) have tried to estimate the number of birds and the amount of time that will be required to approximate the pre-DDT population of Peregrines in the eastern United States, on the basis of a yearly introduction of 250 young and assuming a mortality of 66.6 percent the first year and 20 percent yearly thereafter, an average production of 2 young per successful nesting, 50 percent of all pairs successful each year, and a breeding age of 3 years. The first wild-produced breeders would appear in the population in the 7th year, and by the breeding season of the 15th year, after 4,000 young Peregrines had been released, there would be a breeding-age population of 292 pairs and a total population of more than 1,100 individuals. Obviously, restoration to that extent will not be an easily or quickly accomplished goal, but as Newton (1976) points out in his encouraging editorial, while the ultimate success of domestic breeding programs for conservation occurs only when the released birds themselves reproduce in the wild, such projects should in fairness be judged stage by stage. The first two stages (see Cade 1974b) have been accomplished—domestic production of young and their establishment in nature. The third remains to be achieved.

We can now project fairly accurately how many young Peregrines can be raised by the Peregrine Fund's projects over the next 5 years, the period in which we expect to learn whether the third stage is achievable (table 7). We have estimated these figures on the basis of our experience in breeding Peregrines during the past 4 years and on the basis of the number of falcons we are now holding and will be holding that can be expected to reach breeding age in the next 5 years, adding them to our current breeding stock. The values shown in table 7 also assume an annual average production of 9 eggs per female, 60 percent fertility, 70 percent hatchability, and 95 percent success in raising hatchlings, based on our averaged results since 1973. Obviously, if we can increase fertility, for example, or hatchability, then our annual production will go up at a higher rate. Conversely, if these variables decrease as larger numbers of birds, eggs, and young are handled, production will rise less rapidly. We believe our estimate lies on the conservative side of reality; but in any case

production of sufficient numbers of domestically raised falcons will *not* be the limiting factor on the reestablishment of the Peregrine in the United States, so long as the funds to carry on with mass breeding continue to be forthcoming.

Table 7. Estimated production of Peregrine Falcons for the next five years.

Year	No. Breeding Age Females	No. Laying Females	No. Eggs Laid	No. Eggs Fertile	No. Eggs Hatched	No. Young Raised
A. Actual results in past years						
1973	5	4	41	26	22	20
1974	7	6	59	34	24	23
1975	12	11	109	44	27	26
1976	28	25	191	112	83	69
B. Projected figures for next five years						
1977	40	35	315	186	126	120
1978	49	43	387	228	155	147
1979	52	47	416	246	168	160
1980	66	60	540	324	224	213
1981	75	70	630	378	260	247

ACKNOWLEDGMENTS

Our work has received support from a great variety of sources. We particularly acknowledge the sustained financial help of the National Science Foundation and the World Wildlife Fund over a period of five years. The National Audubon Society has also been generous in support, as have several state and federal agencies, especially the U.S. Fish and Wildlife Service and the Bureau of Land Management. In addition, we thank numerous private individuals, foundations, and conservation organizations for their contributions to the Peregrine Fund. For the use of their birds our special thanks to the following: James Adamson, Vincent Cassone, A. L. Clark, Jerry Craig, James Enderson, Edward Fitch, Richard Fyfe, L. J. Gaeta, James Grier, Fran Hamerstrom, Grainger Hunt, Don Hunter, Henry Kendall, Jeffrey Lincer, Heinz Meng, Jack Oar, Hans Peters, Douglas Pineo, Felix Rodriguez de la Fuente, Martin Schweig, Williston Shor, Philip Shultz, Tom Smylie, John Snelling, Stanley Temple, Brian Walton, Harold Webster, Clayton White, and Jimmy White.

We also thank our co-workers, Phyllis Dague, Bill Heck, Bill Heinrich, and our research collaborators, Bob Berry, Frank Bond, and James H. Enderson, for their enthusiastic help with many aspects of the breeding program.

Literature Cited

Adamson, J. C. 1974. Icrus F[1]—Flying a captive-bred tiercel. *Hawk Chalk* 13(2):32-34.

Beebe, F. C. 1967. Experiments in the husbandry of the Peregrine. *Raptor Res. News* 1:61-86.

Berry, R. B. 1972. Reproduction by artificial insemination in captive American Goshawks, *J. Wild. Manage.* 36:1283-1288.

Bird, D. M., P. C. Lague, and R. B. Buckland. 1976. Artificial insemination vs. natural mating in captive American Kestrels. *Canadian J. Zool.* 54(7):1183-1191.

Boyd, L. 1974. Presentation at the annual meeting of the Raptor Research Foundation, Inc., University of Minnesota, St. Paul.

Boyd, L., and N. Boyd. 1975. Hybrid falcon. *Hawk Chalk* 14(3):53-54.

Burnham, W., and W. Heinrich. 1976. Peregrine Fund—western project-falcon production 1975-76. *Hawk Chalk* 15(3):43-46.

Byron, B. 1972.(*Vide* Dallimore 1972.)

Cade, T. J., ed. 1973. *Peregrine Fund Newsletter* 1:1-6.

———, ed. 1974*a*. *Peregrine Fund Newsletter* 2:1-6.

———. 1974*b*. Plans for managing the survival of the Peregrine Falcon. Pages 89-104 in F. N. Hamerstrom, Jr., R. E. Harrell, and R. R. Olendorff, eds. *Proceedings of the Conference on Raptor Conservation Techniques. Raptor Res. Rep.*, no. 2.

———, ed. 1975. *Peregrine Fund Newsletter* 3:1-6.

———. 1977. The role of captive propagation in the conservation and use of falcons. *International Conference on Falconry and Conservation, Abu Dhabi, 10-18 December 1976* (in press).

Cade, T. J., and P. R. Dague, eds. 1976. *Peregrine Fund Newsletter 4:1-12.*

Cade, T. J., and S. A. Temple. 1977. The Cornell University falcon programme. Pages 353-369 in R. D. Chancellor, ed., *World Conference on Birds of Prey, Vienna 1975, Report of Proceedings.* International Council for Bird Preservation.

Cade, T. J., and J. D. Weaver. 1976. Gyrfalcon X Peregrine hybrids produced by artificial insemination. *J. of the North American Falconers' Assoc.* 15:42-47.

Campbell, J. A., and R. W. Nelson. 1975. Captive breeding and behavior of Richardson's Merlins, 1974. *J. of the North American Falconers' Assoc.* 14:24-31.

Card, L. and M. Nesheim. 1973. *Poultry production*, 11th ed. Lea & Febiger, Philadelphia. Pp. 110-111.

Dallimore, M. J. 1972. Bird of prey breeding attempts at Colwyn Bay. *Captive Breeding of Diurnal Birds of Prey* 1(3):3-4.

Enderson, J. H. 1971. An account of Prairie Falcons bred in captivity—1970. *Raptor Res. News* 5(1):44-47.

Fodor, T. Date unknown. Erfahrungen ueber die Ausbruetung von Wildvogeleiern im Budapester Zoologischen und Botanischen Garten. Aus dem Zoologischen und Botanischen Garten Budapest, pp. 63-66. (Translation 1971 by Foreign Languages Division, Department of the Secretary of State, Canada: Experience with the incubation of wild bird eggs in the Budapest Zoological and Botanical Garden.

Fyfe, R. W. 1976. Rationale and success of the Canadian Wildlife Service Peregrine breeding project. *Canadian Field-Naturalist* 90(3):308-319.

Glasier, P. E. B. 1972. Breeding of birds of prey in captivity. *Captive Breeding of Diurnal Birds of Prey* 1(3):5-6.

Grier, J. W. 1973. Techniques and results of artificial insemination with Golden Eagles. *Raptor Res.* 7(1):1-12.

Jack, A. 1977. The view of falconers. Pages 12-14 in R. D. Chancellor, ed., *World Conference on Birds of Prey, Vienna 1975, Report of Proceedings.* International Council for Bird Preservation.

Kendall, H. 1968. Breeding prairie falcons in captivity. *J. North American Falconers' Assoc.* 7:57-64.

Kenward, R. 1977. Captive breeding—a contribution by falconers to the preservation of Falconiformes. Pages 378-381 in R. D. Chancellor, ed., *World Conference on Birds of Prey, Vienna 1975, Report of Proceedings.* International Council for Bird Preservation.

Koehler, A. 1969. Captive breeding of some raptors. *Raptor Res. News* 3(1):3-18. (English translation from *Der Falkner* 18[1968]: 28-33.)

______. 1970. Red-headed Merlins breed in captivity. *Captive Breeding of Diurnal Birds of Prey* 1(1):16-20. (English translation from *Deutcher Falkenorden*, 1970, pp. 87-92.

Lincer, J. L. 1975. DDE-induced eggshell-thinning in the American Kestrel: A comparison of the field situation and laboratory results. *J. Appl. Ecol.* 12:781-793.

Mendelssohn, H., and U. Marder. 1970. Problems of reproduction in birds of prey in captivity. *International Zoo Yearbook* 10:6-11.

Meng, H. 1972. Breeding Peregrine Falcons in captivity. *Hawk Chalk* 11(2):40-44.

Morris, J. 1972. Peregrine/Saker breeding. *Captive Breeding of Diurnal Birds of Prey* 1(3):14-15.

Morris, J., and R. Stevens. 1971. Successful cross-breeding of a Peregrine tiercel and a Saker Falcon. *Captive Breeding of Diurnal Birds of Prey* 1(2):5-7.

Newton, I. 1976. Raptor research and conservation during the last five years. *Canadian Field-Naturalist* 90(3):225-227.

Nye, A. G., Jr. 1976. Falconry as a sport. *Hawk Chalk* 15(3):34-38.

Olendorff, R. R. 1968. A contribution to the breeding behavior of the American Kestrel in captivity. *Raptor Res. News* 2:77-92.

Peterson, R. S. 1968. The domestic raising of the Peale's Peregrine Falcon. *J. of the North American Falconers' Assoc.* 7:64-67.

Platt, J. B. 1976. Gyrfalcon nest site selection and winter activity in the western Canadian Arctic. *Canadian Field-Naturalist* 90:338-345.

Porter, R. D., and S. N. Wiemeyer. 1970. Propagation of captive American Kestrels. *J. of Wildl. Manage.* 34:594-604.

Santer, C. H. 1972. Kestrel breeding report 1972. *Captive Breeding of Diurnal Birds of Prey* 1(3):22-23.

Shor, W., ed. 1975. The 1975 NAFA field meet. *Hawk Chalk* 14(3):31-33.

Smylie, T., and F. Bond. 1975. A traditional hack of Prairie Falcons. *J. North American Falconers' Assoc.* 14:32-33.

Snelling, J. C. 1973. Lanner Falcons breed in captivity: USA *Bokmakierie* 25:27-33, 50-55.

Temple, S. A. 1972. Artificial insemination with imprinted birds of prey. *Nature* 237:287-288.

______. 1975. Project 986. Western Indian Ocean raptors—ecology and conservation. *World Wildlife Yearbook 1974-75*, pp. 210-212.

Terrasse, J. F. 1972. Association nationale des fauconniers et autorsiers français—Report 1972. *Captive Breeding of Diurnal Birds of Prey* 1(3):1-3.

Trommer, G. 1973. Successful breeding of Lanner Falcons. *Captive Breeding of Diurnal Birds of Prey* 1(4):6.

Waller, R. 1962. Der Wilde Fak ist mein Gesell. Verl. Nermann-Neudamm, Melsungen.

Weaver, J. D., and T. J. Cade. 1974. Special report on the falcon breeding program at Cornell University. (RRF BPIE No. 90). *Hawk Chalk* 13(1):31-42.

Willoughby, E. J., and T. J. Cade. 1964. Breeding behavior of the American Kestrel (Sparrow Hawk) *Living Bird* 3:75-96.

Wrege, P., and T. J. Cade. 1977. Courtship behavior of large falcons in captivity. *Raptor Res.* (in press).

PRELIMINARY ANNOUNCEMENT—1978 ANNUAL MEETING OF THE RAPTOR RESEARCH FOUNDATION. The Board of Directors have accepted an offer from Pennsylvania Raptor Rescue to host the 1978 meetings in Allentown, Pa. Cohosts will include Hawk Mountain Sanctuary and perhaps other local organizations. Pre-meeting activities will begin Friday, November 3, and the conference will culminate with a trip to Hawk Mountain on Monday the 6th. Headquarters will be the Americus Hotel in Allentown, where special rates will be available; all meetings will be held in the Hotel. Local Chairperson is Mrs. W. B. (Hope) Carpenter, R.D. 1, Box 150A, Mt. Bethel, PA 18343. Further details will be circulated early in 1978.

ADVERTISEMENTS

At the 1977 annual meeting, November 11-14 it was announced that paid advertisements would be accepted for publication in *Raptor Research.* Such material will ordinarily be printed at prevailing page costs. Send all such material to the Editor.

Address all matters dealing with membership status, dues, publication sales, or other financial transactions to the Treasurer.

Send changes of address to the Treasurer.

Address all general inquiries to the Secretary.

See inside front cover for suggestions to contributors of manuscripts for *Raptor Research*, *Raptor Research Reports*, and special Raptor Research Foundation publications.